

ADVANCES IN SQUID BIOLOGY, ECOLOGY AND FISHERIES

PART II – OEGOPSID SQUIDS



Rui Rosa • Graham J. Pierce
Ron O'Dor
Editors

Fish, Fishing and Fisheries

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ECOLOGY AND FISHERIES**

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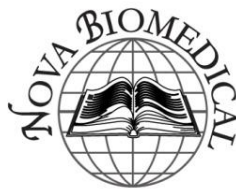
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**ADVANCES IN SQUID BIOLOGY,
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PART II – OEGOPSID SQUIDS**

**RUI ROSA
GRAHAM PIERCE
AND
RON O'DOR
EDITORS**



New York

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***Berryteuthis magister*, Schoolmaster Gonate Squid**

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Abstract

Biology, ecology and fisheries of one of the most highly abundant and wide-spread North Pacific commercially valuable gonatid squid *Berryteuthis magister* have been reviewed, based on the analysis of early life history, age and growth, fecundity and maturation, size-and-maturity, distribution at different ontogenetic stages, feeding habits, population structure, and changes in catch and abundance.

1. Introduction

The schoolmaster gonate squid *Berryteuthis magister* (Berry, 1913) is a wide-spread boreal North Pacific species of the oegopsid family Gonatidae (Nesis, 1973, 1985, 1987, 1995, 1997; Okutani, 1995, 2005; Okutani et al., 1988). This species is highly abundant and plays an important role in various marine ecosystems of the North Pacific Ocean, being prey to numerous predators and exhibiting life style of a predator from the early ontogenetic stages (Chuchukalo, 2006). *Berryteuthis magister* is the only commercially harvested species of the family Gonatidae in the North Pacific Ocean (Nesis, 1998; Roper et al., 2010). This species is unique in many aspects, which is reflected in characteristic patterns of its spatial, vertical and seasonal distribution; age, growth and maturation; intraspecific structure; and behavior (Arkhipkin et al., 1996; Fedorets, 2006; Katugin, 1995a, 1998, 2002; Kubodera, 1992; Nesis, 1998).

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Irrespective of the fact that a huge body of information about this species has been published in the scientific literature, its life cycle remains to a greater part a mystery, because there still is no or very few reliable information about the squid spawning sites, egg-masses and the earliest ontogenetic stages. Most of the available data on *B. magister* comes from the studies of post-paralarval stages, juveniles and adults. Even though the information about *B. magister* is somewhat restricted ontogenetically, it nevertheless enabled the researchers to expand our understanding of various biological traits of this species. In this review, we will consider both published and original information about the species, and pay special attention to those features of the squid biology and fisheries that had been weakly covered in the literature. Most of the data that we have used were collected during research cruises of TINRO-Centre into the boreal North Pacific Ocean in the late 20th – early 21st centuries.

2. Life History Biology

Berryteuthis magister is a benthopelagic species, and its mode of life can be characterized as quasibenthic, indicating that the squid life cycle is strongly associated with the bottom (Okutani, 1988).

In most areas across its geographic range, the species occurs almost exclusively in deep water primarily on the continental slope, which makes it rather difficult to study life history of this squid, in particular, the earliest and latest phases of ontogenesis. Data on spawning and earliest ontogenetic stages of *B. magister* are scarce and often rather controversial.

Nevertheless, critical assessment of the existing data makes it possible to reconstruct a reliable version of the species life history.

2.1. Early Stages

Direct observations on spawning and hatching of *B. magister* have never ever been recorded. The only reliable information on presumably *B. magister* egg masses comes from the coastal waters off southeast Alaska (Bruce Wing, pers. comm.).

These egg masses were described as brown-colored gelatinous spheres 25-50 cm in diameter and tapering on the top; they were observed drifting below the surface to about 15 m depths in January through March. Individual eggs were ovoid in shape (1.7 by 2.0 mm) inside colorless spherical outer capsule of about 2.5-3.0 mm in diameter.

Those eggs from floating egg masses appeared very close in size to the known size of ripe eggs from oviducts of spawning and spent *B. magister* females from the northwestern Bering Sea, which ranged 2.50-3.22 mm in diameter (Nigmatullin et al., 1996). Judging from the egg size and occurrence of spawning *B. magister* females in the area where egg masses have been observed, these egg masses most likely belong to this particular species.

In the Northeast Pacific, spawning of the species was indirectly evidenced by the occurrence of recently hatched individuals. In the Strait of Georgia, the smallest reported paralarvae were 4.9 mm in mantle length, had dome-shaped mantle without developed fins, internal yolk, relatively large funnel and only three pairs of small appendages; they were captured from February through April (Okutani, 1988).

These and larger paralarvae with mantle length of up to 7 mm with better developed arm crown were captured by samplers towed obliquely from 5 m above the seafloor at depths 300-400 m. In the northern Gulf of Alaska, early life stages of the Gonatidae identified as *B. magister* ranged in mantle length from 3.4-12.3 mm, were distributed mostly over the shelf break or troughs and did not show the diel pattern (Jorgensen, 2007). These individuals were captured in tows made double-obliquely to a maximum depth of 300 m. In other Northwest Pacific areas, early stages of *B. magister* were also taken in gear towed from the bottom (Arkhipkin et al., 1998). In their research of the Gonatidae early life stages distribution across the boreal North Pacific, the authors noted that there were difficulties in species identification of early stages, which they placed under the name “*Berryteuthis magister*”, and that some of them were most likely *Gonatus tinro*, while others were presumably *B. magister* (Kubodera, Jefferts, 1984). Therefore, the existing reliable data on occurrence of *B. magister* earliest life stages suggest that, most likely, after hatch young squid remain near the bottom for some time and do not show up in the upper water column.

Data on the life style of post-paralarval and early juvenile stages of *B. magister* vary among different authors. According to detailed information collected during the Okhotsk Sea pelagic and bottom trawl surveys, the smallest *B. magister* with 46 mm mantle length were captured in bottom trawls, and young squid start vertical migrations having reached 140-160 mm mantle length (Nesis, 1989). In the northwestern Bering Sea, *B. magister* juveniles ranging from 40-120 mm mantle length occur primarily near the bottom at depths 300-450 m (Fedorets, 1986; Nesis, 1995). However, in the northwestern Bering Sea in autumn, *B. magister* juveniles with mantle lengths 38-78 mm were found in the epipelagic layer above the outer shelf and slope only at night (Gorbatenko et al., 1995). Obviously, young squid were descending from the epipelagic zone to deep layers during daytime, which is an indication that micronektonic juvenile squid of that size already conduct diel vertical migrations. Comparative data from bottom and midwater trawl surveys revealed that, in the northwestern Bering Sea, juvenile *B. magister* occurred at 80-200 m above depths 180-2000 m at night, disappeared from pelagic catches and were distributed close to the bottom at depths 380-500 m during daytime; most likely, squid start vertical migrations at mantle length about 20-30 mm and continue diel migrations at mantle length 70-120 mm (Arkhipkin et al., 1998). The critical point here is when these migrations become less explicit, and at what size do the squid start living exclusively close to the bottom. There is also no common view on the question at what size do young *B. magister* start and finish ontogenetic descend.

Nesis (1995, 1998) suggested that some squid start descending at approximately 60-80 mm mantle length, and pelagic phase of *B. magister* life cycle is completed when squid reach approximately one half of their definitive adult size, which is 140-160 mm mantle length in the Okhotsk and western Bering Sea. In his hypothetical scheme of *B. magister* life cycle, Kubodera (1982) suggested that, after hatch, the earliest stages inhabit the upper layers until they grow to about 16-17 mm in mantle length, when they start ontogenetic descent, and at about 50-70 mm mantle length they start benthic life. However, considering that there were no reliable records of *B. magister* early life stages in the surface layers and all records of the hatchlings are associated with bottom tows, it is likely that, after hatch, which occurs on or near the bottom, young squid remain demersal and do not show up in the upper layers until they become swimmers good enough to conduct diel vertical forage migrations.

To sum it up, *B. magister* is a bottom spawner, and in their early and late life history squid are demersal.

Females produce large oval egg masses of up to 50 cm in diameter, and presumably attach them to the bottom by a small “pig-tail”. In case egg masses are detached from the substrate (e.g., by strong currents), they float near the bottom or in the water column due to neutral buoyancy. Eggs remain in the gelatinous media of egg mass during the entire embryogenesis, and hatch into free floating paralarvae, which are about 3.5 mm mantle length at hatch and live presumably close to the bottom until they develop arm crown consisting of four pairs of arms and a pair of catching tentacles, which happens at mantle length of about 7 mm. Having grown to about 20-30 mm mantle length, young squid begin diel vertical migrations, ascending to the subsurface layers at night and descending back to near-bottom layers during daytime. Squid continue regular vertical migrations into the upper pelagic layers until they grow to at least 70 mm mantle length or somewhat larger, and then they gradually turn into almost exclusively bottom dwellers. They may continue to conduct forage migrations into the mesopelagic zone occasionally (not on a regular diel basis), and very rarely appear in the epipelagic layers.

2.2. Age and Growth

Since direct observations on growth of pelagic squid is rather difficult (Jackson, 1994), age and growth estimations for these animals are based on a variety of indirect methods, which in many cases lead to controversial results. In this respect, *B. magister* is an example of a wide spectrum of age assessments, and therefore of disagreements in life span estimates. Studies, based on monthly size and maturity progression suggested that the species life cycle duration is either one (Jefferts, 1986; Naito et al., 1977a) or two (Nesis, 1989; Railko, 1979, 1983; Railko et al., 1996; Yuuki, Kitazawa, 1986) years. Application of hard age-registration structures, such as statoliths and gladii, produced even more inconsistency in age estimates for *B. magister*. Combined application of these two structures yielded compatible results: immature squid with mantle length 225-233 mm from the ocean off the Kuril Islands were aged 263-265 days using statoliths and 230-268 days using gladii, implying that the squid lives about one year (Arkhipkin, Bizikov, 1991; Bizikov, 1991). Involvement of squid with a wide size range (26-369 mm mantle length) from early juveniles to spawning adults suggested that postembryonic life of *B. magister* lasts from 13-14 to 16 months in the northwestern Bering Sea (Arkhipkin, 1996; Arkhipkin et al., 1996). In that study, numbers of growth increments of statoliths and gladii were concordant for all life stages, from early juveniles (35-40 mm mantle length) to mature adults (280-330 mm mantle length). Similar results obtained from two independent structures indicated that the revealed age and growth patterns were reliable.

These and other studies on the squid ageing were contradictory to the study, where life duration of *B. magister* from the Japan and Okhotsk seas was estimated to be four years based on statoliths microstructure (Natsukari et al., 1993). Such a large discrepancy between the assessments could be due to a system error, when the increments that are deposited not on a daily basis were counted as daily, or when the fine bands, considered as daily rings, were in fact false due to optical interference. The results showing that *B. magister* lives in-between one and two years seem more reasonable, in particular, because assessments from statoliths microstructure were validated by data from gladii and growth-increment analysis of successive modal classes (Arkhipkin et al., 1996).

In addition, experiments of rearing the squid early life stages in captivity at sea confirmed that “second-order” increments, which counts suggested a 13-16 month life span of *B. magister* after hatch, were deposited on a daily basis (Arkhipkin, Bizikov, 1997).

It is likely that, in the Japan Sea, where *B. magister* lives at colder water temperatures, produces somewhat larger eggs and grows to generally smaller sizes, the species life cycle pattern does not differ dramatically from that of notably larger squid inhabiting other areas of the North Pacific. Indeed, though individuals from Rebun Bank (Japan Sea) performed lower growth rates (and hence size-at-age) than individuals from Kitamiyamoto Bank (southwestern Okhotsk Sea), squid from these two areas were similar in life span (Natsukari et al., 1993). On the other hand, it was shown that life duration may differ for squid hatched in different seasons, and, in the northwestern Bering Sea, summer-born individuals matured earlier (the majority of spent animals were aged 12-14 months) than autumn-born individuals (the majority of spent animals were aged 13-14 months, and the oldest were 16 month old) (Arkhipkin et al., 1996). Taking into account large eggs and long time needed for embryonic development in cold waters of the Subarctic Pacific, the total life span of *B. magister*, including embryonic and post-embryonic phases, lasts most probably about two years.

Reliable information on *B. magister* growth was obtained for animals from the northwestern Bering Sea (Arkhipkin, 1996; Arkhipkin et al., 1996). It was shown that the growth curves (of mantle length versus days) for *B. magister* females and males were best fitted by logistic growth curve functions and were “S”-shaped, suggesting that growth rates were slower in early and late days of life, and faster in-between. Absolute growth rates were the fastest in females at the age of 210-270 days (1.05-1.08 mm per day) and in males at the age of 180-210 days (about 0.9 mm per day). Males and females grew at similar rates until they were 210-240 days old, then males grew slower, and at the age of 390 days their average mantle length was about 50 mm less than that of females. These data showed that somatic growth was the highest in actively foraging young and immature animals, and decreased in the latest stages, when the accumulated energy is invested into gonad development.

2.3. Maturation and Fecundity

In spite of large amount of information collected on *B. magister*, reproductive biology of the species is still rather poorly studied. Initially, the following reproductive characters were reported for *B. magister* from the Japan Sea: mature ova were measured only 1.5-2.0 mm in diameter; and copulation on the inner wall of female mantle was suspected (Kasahara et al., 1978). Later, ripe oocytes were reported to be in fact 4.0-5.0 mm in diameter, spermatangia (=spermatophores) were found to be implanted in the female inner mantle wall, and female fecundity was assessed at about 5 thousand eggs (Nazumi et al., 1979).

It was also suggested that females spawn out ripe eggs in portions (Railko, 1979; Yuuki, Kitazawa, 1986). In mature females from the northwestern Bering Sea, the size of mature eggs was first measured as 3.5-4.5 mm, and fecundity was assessed at 3.3-7.2 thousand eggs in females with mantle length 230-250 mm, and 23-30 thousand eggs in females with mantle length 340-380 mm (Fedorets and Kozlova, 1986). Further scrupulous analysis of reproductive characters of *B. magister* from the northwestern Bering Sea yielded somewhat different estimates: eggs were in fact a little smaller and fecundity much higher (Nigmatullin et al., 1996).

Ripe eggs in oviducts of prespawning females were measured 2.5-3.26 mm (2.97 ± 0.20 mm, on the average) in diameter, and in oviducts of spawning and spent females 2.5-3.22 mm (2.86 ± 0.25 mm, on the average). Individual absolute fecundity ranged from 20-25 to 90-95 thousand eggs. In prespawning females with mantle length 230-290 mm it varied from 27 to 60 thousand eggs (40 thousand eggs, on the average). In spawning and spent females of the same size range from 13.8 to 37 thousand eggs (27 thousand eggs, on the average) remained unspawned, which meant that realized fecundity was about 30% of the absolute fecundity. The same authors also analyzed reproductive characters of *B. magister* males (Nigmatullin et al., 1996). It was shown that the length of mature spermatophores varied significantly from 12 to 21 mm, and larger males have longer spermatophores. The Needham's sac can hold as much as 496 spermatophores (in the male with mantle length 210 mm), and the number of spermatophores produced by a single male during its mature stage was assessed as at least 600-700 and probably up to 1000.

In *B. magister*, males mature at smaller size and at younger age than females. Therefore, adult males are usually smaller than females in all areas of the species wide range: Japan Sea (Yuuki, Kitazawa, 1986), Okhotsk Sea (Nesis, 1989), western Bering Sea (Nesis, 1995), Gulf of Alaska (Kubodera, 1992). Maturation in *B. magister* occurs at a relatively slow pace, during several months. For example, in the northwestern Bering Sea, at mantle length about 100-150 mm and age 200-250 days, males and females were immature; however, all males larger than 200 mm mantle length and older than 310 days were mature and some of them already spawning, and most females larger than 265 mm and older than 350-370 days were mated and thus ready to produce egg masses (Arkhipkin et al., 1996).

Our data suggested that immature squid of both sexes have similar sizes, and in the beginning of maturation females begin to grow faster than males, gaining ultimately much larger definitive size (size at full maturity); also, squid from different parts of the species geographic range display regional-specific size-at-maturity characters (Table 1). Animals from the Japan Sea mature at the smallest size: females at about 200 mm and males at about 160 mm mantle length. There was an evident trend towards an increase in size-at-maturity from the north to the southwest and southeast in the North Pacific (excluding Japan Sea). Individuals inhabiting the northernmost areas (the northwestern Bering Sea) mature at a relatively small size: females at about 260 mm and males at about 210 mm mantle length. The squid from Pacific waters off the south and central Kuril Islands are, on the average, somewhat larger than those from off the north Kurils and East Kamchatka, and comparatively large squid are found in the Northeast Pacific, where females mature at about 280 mm and males at about 230 mm mantle length.

Assignment of squid to a particular maturity stage reflects the actual state of gonad development, and depends upon other factors, such as the maturity scale used by a researcher. Most of suggested maturity scales, even the so-called "universal" ones, have been developed for cephalopods with small- or medium-sized eggs (Juanico, 1983). The universal principles used for development of maturity scales in cephalopods (Burukovskiy et al., 1977; Lipinski, 1979) should be species-adapted, in our case, to *B. magister*, and should take into account specific traits in reproductive biology of this high-latitude demersal species with rather big ripe eggs. Nigmatullin et al. (1996) argued that, in case of *B. magister*, the application of such universal scales created certain difficulties, particularly in attempts to fine-tune the stage, defined by cyto- and histological criteria, with recognizable macroscopic characters of gonad development.

Table 1. Size-at-maturity of *Berryteuthis magister* from different regions of the species geographic range

Region	Females					Males				
	I	II	III	IV	V**	I	II	III	IV	V
Japan Sea	112.5 ±1.1	168.5 ±0.4	187.3 ±0.5	210.1 ±5.0	223.1 ±3.4	112.6 ±1.1	148.7 ±1.2	154.0 ±0.6	161.4 ±0.4	165.2 ±2.1
Off South Kuril Islands	155.0	230.4 ±1.7	273.3 ±3.8	292.2 ±7.7	282.6 ±13.2	145.9 ±3.3	199.9 ±2.1	220.9 ±2.1	226.0 ±2.2	244.1 ±1.8
Off Central Kuril Islands	192.9 ±3.0	227.8 ±0.4	261.5 ±0.7	282.6 ±0.8	302.6 ±3.4	182.8 ±3.4	207.9 ±0.6	215.1 ±0.6	220.4 ±0.5	227.0 ±1.0
Off North Kuril Islands	163.5 ±2.3	216.7 ±0.5	250.4 ±0.8	261.5 ±1.9	271.2 ±2.2	165.4 ±1.3	196.5 ±0.5	207.4 ±0.8	215.4 ±0.7	216.9 ±1.1
Okhotsk Sea	139.5 ±1.4	169.8 ±1.8	246.6 ±6.7	276.4 ±8.6	331.6 ±5.7	136.1 ±1.1	169.4 ±1.2	208.1 ±3.8	224.9 ±3.0	235.5 ±2.9
Off East Kamchatka	131.6 ±2.7	224.9 ±1.7	257.2 ±3.0	267.0 ±13.2	265.2 ±8.0	140.6 ±2.7	189.4 ±3.9	204.1 ±3.5	211.5 ±2.5	215.7 ±2.0
Off Commander Islands	155.8 ±4.4	231.5 ±0.9	257.4 ±1.1	269.7 ±3.2	266.6 ±1.1	148.2 ±2.8	201.1 ±1.7	217.1 ±1.0	215.7 ±0.8	217.8 ±0.5
Western Bering Sea	141.1 ±2.0	214.5 ±0.8	245.7 ±0.5	260.9 ±0.4	255.3 ±1.9	144.7 ±0.9	191.7 ±1.0	206.0 ±0.8	214.3 ±0.4	210.9 ±0.8
Eastern Bering Sea*	177.1 ±7.9	203.3 ±1.1	248.3 ±12.8	350.5 ±23.5	*	181.2 ±1.9	193.7 ±1.4	210.1 ±8.4	236.7 ±7.9	*
Off Aleutian Islands	152.5 ±3.2	197.3 ±1.8	248.5 ±4.3	266.5 ±7.1	296.3 ±3.4	161.1 ±1.9	196.5 ±2.2	206.6 ±3.6	230.8 ±8.1	248.0 ±6.7
Gulf of Alaska	145.5 ±3.6	200.2 ±2.2	258.0 ±4.1	281.4 ±5.8	302.9 ±7.3	154.7 ±2.1	191.0± 2.2	202.3± 5.2	226.7 ±4.2	246.0 ±7.5

*no spawning individuals have been analyzed.

**stage V includes both spawning and spent females.

These authors suggested detailed maturity scale for this species. Seven basic maturity stages of *B. magister* reproductive system were defined: immature (stages I and II), physiologically maturing (stage III), physiologically mature (stage IV), functionally mature (stage V, three substages), spawning (stage VI) and spent (stage VII). Though this scale provides a new insight into reproductive biology of *B. magister*, most data at hand have been collected and analyzed using less sophisticated approach.

For example, Japanese scientists use a simple 3-stage subdivision of the squid maturity: immature, maturing and mature, adding gonadosomatic index (GSI) as a metric control of maturity (Kasahara et al., 1978; Kubodera, 1992; Naito et al., 1977a; Nazumi et al., 1979; Yuuki, Kitazawa, 1986). Some Russian researchers first used 4-stage scale: stage I (immature), stage II (onset of maturation), stage III (maturing) and stage IV (mature, including spawning and spent) (Shevtsov, 1971).

However, later they shifted to a more detailed 6-stage scale, when former stage IV has been split into three separate stages to better estimate spawning event: stage IV (mature), stage V (prespawning and spawning; three substages; mating occurs at this stage, usually at substage V₂) and stage VI (spent).

The use of GSI in the study of *B. magister* reproductive biology proved to be a reliable but not very informative substitute for rather artificial (and frequently dubious) subdivision of gradual changes upon maturation into separate stages. In the southwestern Japan Sea, GSI was about 2.0 in most immature females, and ranged from 15.5–28 (19.8, on the average) in mature females with a mean mantle length 180 mm; in males GSI gradually increased and did not exceed 2.8 (Yuuki, Kitazawa, 1986). Unfortunately, the use of GSI shows only trends in maturation, and does not reveal specific traits in the process, morphology and physiology of maturation, concealing important events and changes in reproductive system that happen during maturation. Some authors also used information derived from the size of nidamental and oviducal glands as additional information on maturity stage of female *B. magister* (Katugin, 1998; Kubodera, 1992; Kubodera et al., 1983; Nigmatullin et al., 1996).

An important issue associated with *B. magister* reproductive behavior is whether there exists hectocotylization in males of this species. Kasahara et al. (1978) did not observe hectocotylization in *B. magister* males from the Japan Sea. Later, changes in morphology of the distal portion of one of ventral arms upon maturation were described as hectocotylization in males from the northeastern Pacific Ocean, Bering Sea (Voight, 1996), and Japan Sea (Katugin, 1998, 2000). Nesis (1996, 1997) disagreed that these changes in ventral arm morphology constitute a true hectocotylus (arm modification, which serves for transfer of spermatophores), and suggested that, during mating, males use their long distensible penis to pass spermatophores and implant them into the inner wall of female mantle. However, our unpublished data show that penis (anterior portion of the Needham's sac) in *B. magister* is relatively short, and its terminus does not reach the anterior margin of the mantle even in spawning males. On the other hand, the area with modified suckers (=hectocotylus) stretches from about 40 to 70 mm from ventral arm base, which is pretty close to the observed depth of attachment of sperm bulbs inside female mantle: copulations are implanted as deep as about 65 mm from anterior mantle margin. These observations indirectly indicate that modified arm is used to place spermatophores inside female mantle cavity.

In *B. magister*, mating occurs immediately prior to spawning; therefore, the occurrence of mated animals is an indicator of close proximity of spawning grounds. Normally females mate at stage V (substage V₂), when their oviducts are full with ripe eggs. Having produced egg mass after first mating, many females mate the second time. Females with three copulations occur relatively infrequently. On the western Bering Sea slope, we have observed a very unusual phenomenon, when, in the absence of mature males for some unclear reasons, females at stage V (substage V₂) that had not been mated (without signs of copulation) began spawning out unfertilized eggs. Typically, during spawning season, sex ratio is uneven with females outnumbering males (judging from trawl catches); nevertheless, there are usually enough males to mate with, and ready-to-spawn females mate successfully.

The use of external characters of reproductive system (gonad external morphology development of accessorial organs in females such as nidamental glands secreting mucous media for egg-mass formation, evidence of mating in females and hectocotylization in males), and application of existing scales for assessments of maturity eventually provided valuable information on *B. magister* reproductive biology. Taking into consideration all these sets of information, we may suggest a pretty reliable pattern for the squid maturation, mating and reproduction, which will be as follows. In post-paralarval stages, young squid actively feed and gain size through the rapid somatic growth, and actively growing animals long remain immature until they start to develop their reproductive organs (gonads, gonoducts and other

organs, such as nidamental and oviducal glands in females). Such a transition from immature condition (stage I) starts at approximately the same time and size in both sexes, and at the onset of maturation state (stage II), females become somewhat larger than males in all stocks across the species range. At that stage males begin to develop modifications on the ventral arm, which will further become a hectocotylus. Males grow slower and mature faster and earlier than females. Size difference between sexes becomes more and more pronounced as the squid grow and mature. Processes of maturation in *B. magister* have been thoroughly studied in animals from the Northwest Pacific (Reznik, 1981a,b, 1982, 1983; Nigmatullin et al., 1996).

First early spermatocytes start to appear in immature males (stage I), and spermatophorogenesis starts at the onset of maturation (stage II), when spermatophore complex of organs begins to function. The transfer from stage II to the next stage is rather rapid and, at the latter stage, the growth of males slows down, so that they almost reach their definitive size. At stage III first pseudo-spermatophores (undeveloped spermatophores) appear in the spermatophore (Needham's) sack, and males develop a well-defined hectocotylus, which becomes morphologically evident as modification of dorsal and mediodorsal sucker rows (swelling at base of sucker stalks) in the middle portion of one ventral arm (extremely rarely on both ventral arms) (Katugin, 2000). At later stages, mature spermatophores are packed and stored in the Needham's sack, ready to be injected out of the penis onto the modified ventral arm and then further transferred to a female during the course of copulation.

The process of maturation in females is more protracted than in males. In the gonad of immature female (stage I), the oocytes experience protoplasmic growth, and their number is already determined, so that the absolute fecundity can be assessed. At the onset of maturation (stage II), trophoplasmic growth, or vitellogenesis of oocytes begins. Yolk accumulation continues relatively evenly in oocytes all over the ovary at the next stage (III). During further step of maturation (stage IV), trophoplasmic oocytes form a separate cohort, at first less numerous than the cohort of protoplasmic oocytes. At this stage, the ovary becomes full of ripe semi-transparent eggs, but the oviducts are empty. Size structure of oocytes in mature ready-to-spawn females (stage V and higher) is roughly bimodal: small protoplasmic oocytes (0.3-0.9 mm in diameter) and large vitellogenic oocytes (2-3.5 mm in diameter), the latter filling up not only the gonad but both oviducts as well. Having gained such a condition (stage V, substage V₂), a female is ready to copulate with a male. At this stage ripe eggs from the ovary and oviducts weigh 5-6% of female's body weight, and a female starts to squeeze eggs from the oviducts, fertilize them in mantle cavity, and spawn them out in a form of a large egg-mass. Active, protracted and portioned spawning can be assigned to a separate condition in maturation process of a female (stage VI). Traces of mating (=copulation) are located inside mantle cavity of a spawning female: there are usually one or two, rarely three packs of sperm ropes implanted into the inner mantle wall (rarely into gill or midgut gland). During spawning, a female experiences serious changes in morphology: mantle wall becomes very thin, tentacles are lost, midgut gland sharply decreases in size. Spent female (stage VII) has almost empty gonad (which appears as a dark yellow band) and oviducts, with numerous degenerated vitellogenic oocytes (certain number of gaining yolk oocytes are resorbed during maturation) and with most of ripe eggs already spawned out. Therefore, in *B. magister*, development of the ovary is asynchronous and discontinuous, and the actual or ultimately realized fecundity is largely determined by the established pool of yolk oocytes.

Rough estimates suggest that realized fecundity in this squid species ranges from 10-50% (30% on the average) of the absolute individual fecundity, and though more than 80% of all oocytes reach vitellogenesis, only 35% of yolk oocytes ripe and are spawned out during egg-mass formation (Nigmatullin et al., 1996).

3. Ecology

3.1. Distribution

Geographic range of *B. magister* corresponds to the following major large-scale zoogeographic subdivisions of the North Pacific: 1) boreal zone (high-boreal sub-zone, including transition waters with adjacent sub-zones, and partly low-boreal sub-zone) and 2) Aleutian-Kamchatka province with four adjacent provinces (Oregon and partly California provinces in the east, and Ainu and partly Sino-Japanese provinces in the west) (Nesis, 1985).

The species range generally fits within the scheme of currents and distribution of water masses in the Subarctic Pacific (Dodimead et al., 1963), and is trans-Pacific with similar abundance and occurrence in the Northwest and Northeast Pacific (Okutani et al., 1988). In the Northwest Pacific, the squid southernmost occurrence is in the Japan Sea off Oki and Tsushima islands (35°25'N).

The squid range stretches along the entire Japan Sea slope, includes off-shore Jamato, Sinoki, Rebun, Oki and Noto underwater rises, and is bounded by shallow Tatar Strait in the north (Ogata et al., 1973; Kasahara et al., 1978; Nazumi et al., 1979; Natsukari et al., 1993; Shevtsov, 1988). The squid occurs almost everywhere on the slope in the Okhotsk and Bering seas (Nesis, 1987; Okutani et al., 1988), and its northernmost occurrence is in the Bering Strait (Jefferts, 1983). The squid dwells along the Pacific Rim from Tohoku (off northern Honshu) (Naito et al., 1977b), off the Kuril and Aleutian islands to the Gulf of Alaska, including deep passes off southeast Alaska and British Columbia, and further down to Monterey Bay in California (Berry, 1913; Bernard, 1980; Nesis, 1987; Kubodera, 1982).

Occasionally, young squid were taken far off-shore in the western Subarctic Current in the area bounded by 42°N and 51°N and 162°E and 177°E (Kubodera et al., 1983; Jefferts, 1983). This is a cold water holosubarctic species, which occurs mainly in Subarctic Water Mass and adjacent transition waters (Jefferts, 1983). Indeed, these squid live in deep water at low temperatures: 1.0-3.6°C in the Bering Sea, 2.0-4.0°C in the Okhotsk Sea and off Kuril Islands, 0.2-1.5°C in the Japan Sea (Fedorets, 1979; Railko, 1979), and only near the surface, there were several captures at a higher temperature of up to 9.6°C (Kubodera et al., 1983).

Patterns of spatial and vertical distribution of *B. magister* at different ontogenetic stages have been studied using database collected in TINRO-Centre expeditions to the Okhotsk Sea and adjacent areas of the Northwest Pacific.

In the pelagic Okhotsk Sea, *B. magister* occurred irregularly and evenly, most frequently off southwest Kamchatka, in the northern areas and off eastern Sakhalin, and occasionally in the southern basin, and was present only close to the Kuril Chain in the ocean (no off-shore records), with maximum distribution density of about 6 thousand individuals per square km in the north of the sea (Figure 1). Near the bottom beyond the shelf, *B. magister* occurred regularly and at high density (Figure 2).

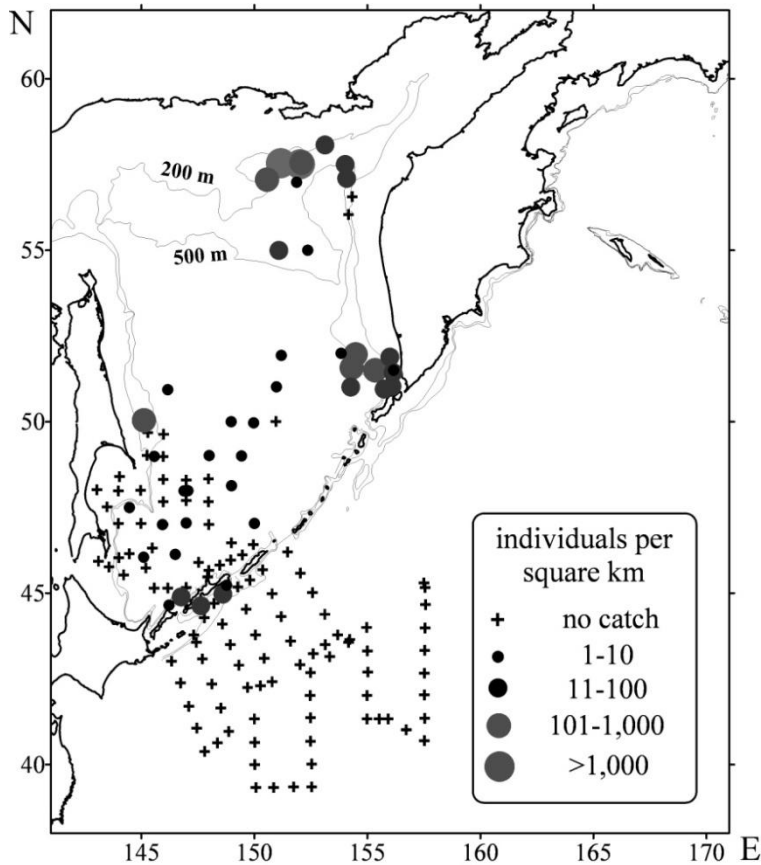


Figure 1. Distribution density of *Berryteuthis magister* in the pelagic zone in the Okhotsk Sea and adjacent North Pacific Ocean.

Maximum density of the squid near the bottom was much higher than in the pelagic zone, of about 54 thousand individuals per square km off southwestern Kamchatka. Pelagic and bottom distribution patterns of juveniles with DML less than 80 mm appeared congruent, most likely due to the fact that, at these sizes, squid are still active vertical migrants. Larger immature adults with DML 90-160 mm occurred predominantly near the bottom along the slope and were captured in the pelagic layers only occasionally suggesting that they are already almost exclusively near-bottom dwellers. Squid at the latest maturity stages occurred exclusively on the slope in the Okhotsk Sea and along the Kuril Islands, forming increased concentrations off southwestern Kamchatka, in the north of the sea and off southeastern Sakhalin.

Earlier studies suggested that, in the Okhotsk Sea mesopelagic zone, juveniles and immature adults of *B. magister* formed dense concentrations just above the slope between 400 m and 600 m depth contours, with peak catches at 450-500 m (Ilyinskyi, 1991). In the upper epipelagic zone (0-60 m), even juvenile *B. magister* were extremely rare, and most juveniles and adults were encountered in the meso- and bathypelagic zone and close to the bottom during greater part of the year (Lapko, 1995; Didenko, 1991a). Therefore, in the Okhotsk Sea, *B. magister* live in deep areas near the bottom during greater part of life, showing up in the pelagic zone only at the early stages.

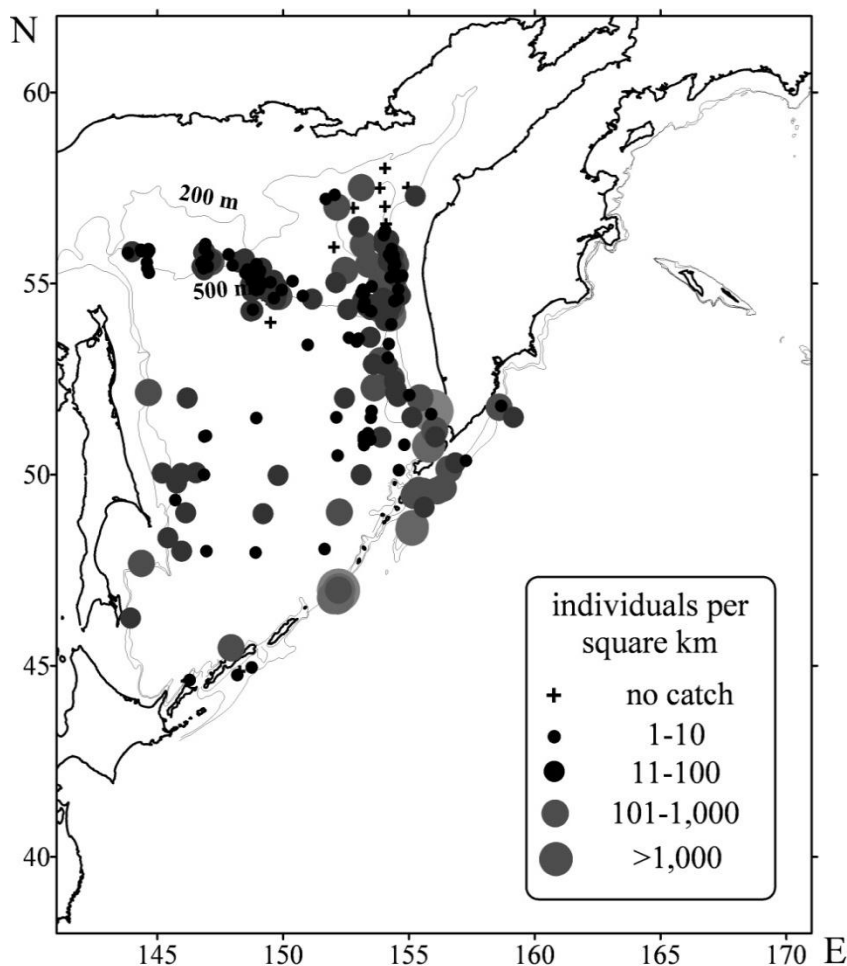


Figure 2. Distribution density of *Berryteuthis magister* near the bottom in the Okhotsk Sea and adjacent North Pacific Ocean.

Such a mode of life is observed in *B. magister* inhabiting other parts of the species range, e.g., in the Bering Sea and Pacific Ocean, squid are encountered primarily on the slope, occur regularly in the mesopelagic zone, and only juveniles occasionally occur in the epipelagic layers (Arkhipkin et al., 1996; Didenko, 1991b; Katugin, Zuev, 2007; Katugin et al., 2006; Naito et al., 1977b; Nesis, 1995; Nesis, Nikitina, 1995; Radchenko, 1992).

Typically, the densest commercial aggregations of squid occur on relatively steep continental slope in areas adjacent to rather narrow shelf and are associated with quasi-stationary local eddies, which are formed in the result of interaction between large-scale (geostrophic) currents and local tidal activity with specific geomorphological structures in each of the fishery areas considered (Malyshev, Railko, 1986; Railko, 1983).

Bathymetric distribution of *B. magister*, based on data collected in August-December 2008 off the Simushir Island (central portion of the Kuril Chain slope), suggests that, during daytime, squid occur near the bottom mainly at depths 350-380 m, migrate to deeper areas at night, and, by the early morning, are found in a wide depth range on the slope and shelf, concentrating near the bottom at depths 180-220 m (Railko P.P., pers. comm.) (Figure 3).

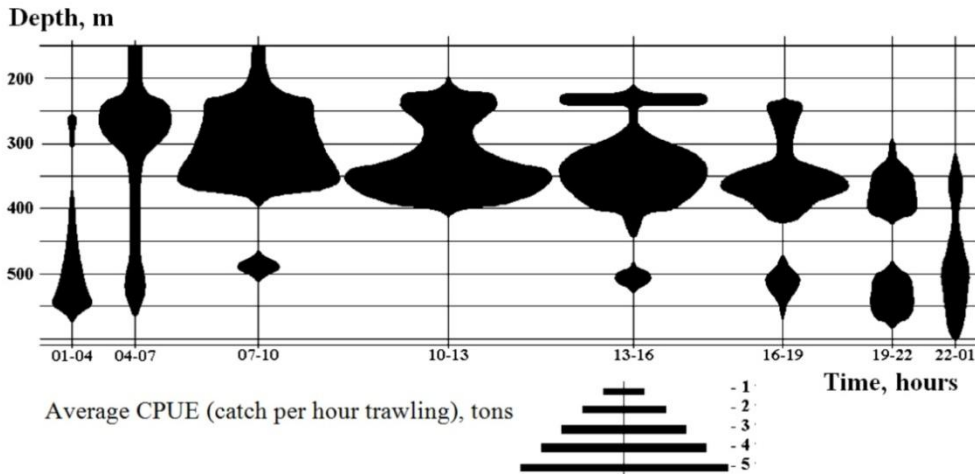


Figure 3. Diel bathymetric distribution of *Berryteuthis magister* off the Kuril Islands.

It is characteristic of *B. magister* that individuals at various ontogenetic stages, from early juveniles to pre-spawning adults occur practically within the same areas along the continental slope in the boreal North Pacific.

Therefore, the squid spawning range roughly corresponds to the species range, and extends along the continental slope in the boreal North Pacific (Figure 4). Individuals at early life stages, though tending to remain within the spawning sites, may be transported with locally prevailing currents far off-shore; however, those that find themselves in the open ocean above the abyssal depths are most likely doomed to die, because they will fail to start demersal life.

Such far moving “doomed” individuals expand the out-cast portion of the species geographic range over wide off-shore oceanic areas in the North Pacific. To continue their life cycle, juvenile squid need to descend to the upper slope within the depth range of about 200-600 m, which is a relatively narrow bottom area.

Those youngsters that were “lucky” to start demersal life in the deep sea near the bottom eventually grow into adults presumably not far from their natal areas. Having reached the adulthood, immature and maturing individuals recruit into aggregations, some of which are harvested commercially.

It is therefore not surprising that fishing grounds for *B. magister* are distributed all over the species range, and both immature and mature squid can be found in one haul. Migratory activity has been suggested for young and actively growing squid in some areas, e.g., along the northern Bering Sea slope (Arkhipkin et al., 1998) and along the slope off the Kuril Islands (Alexeyev, 2007).

However, such activity does not affect very much the functional structure of the species range, since it is associated primarily with forage migrations from the bottom into the mesopelagic layers or along the slope in vertical and horizontal directions.

Moreover, in spite of the existence of forage migrations and a pelagic phase early in the life cycle with a high potential for dispersal over vast areas, there exists a stock structure in *B. magister*, which is supported by morphologic and genetic evidence (see below, 3.5). Such a structure could be maintained given the ability of squid to reproduce in areas of origin.

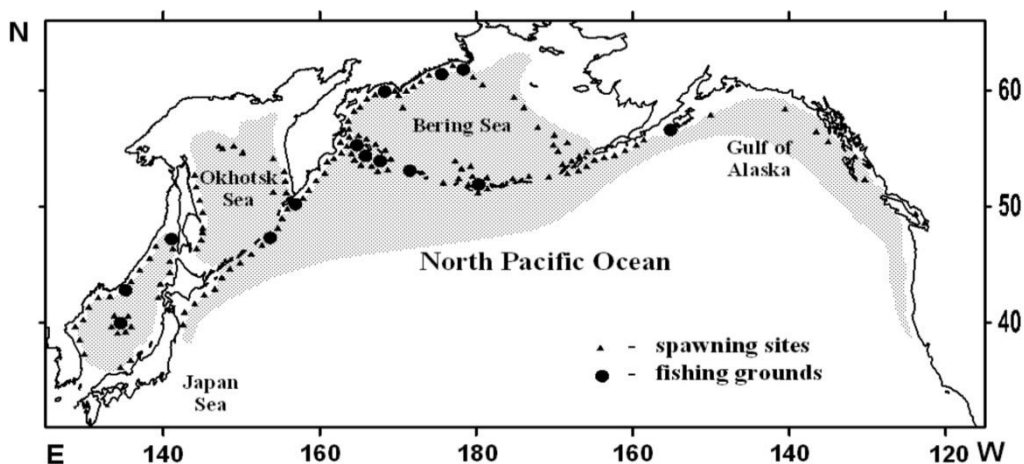


Figure 4. Distribution range of *Berryteuthis magister* showing general occurrence (shaded area) and location of spawning sites and fishing grounds.

3.2. Size-and-Maturity

There was a geographic pattern in size and maturity of *B. magister* from different areas. We have studied monthly changes in size structure of squid aggregations and associated distributions of squid at different maturity stages to obtain seasonal patterns for the examined geographical populations. Squid from the following regions were analyzed in that respect: the Japan Sea (aggregations from the slope along the Asian coast and from the banks in the centre of the sea), the Okhotsk Sea, Pacific Ocean off the Kuril Islands and East Kamchatka, banks around the Commander Islands, the Bering Sea and Northeast Pacific (eastern Aleutian Islands and Gulf of Alaska).

A separate geographic subspecies *B. magister shevtsovi* inhabits the Japan Sea, and is characterized by notably smaller size-at-maturity than the squid from conspecific populations living in other regions of the North Pacific (Katugin, 2000). In the Japan Sea, squid are distributed mostly in-between the shelf-break and down to 1000 m and even deeper with the densest concentrations within the depth range from 300-500 m (Kasahara et al., 1978; Nazumi et al., 1979; Okiyama, 1993; Shevtsov, 1988; Yuuki, Kitazawa, 1986). Within the sea, there exists variability in size structure and maturity patterns of the squid (Figures 5-8). Patterns of seasonal progression in size and maturity obtained for *B. magister* inhabiting different parts of the Japan Sea, from the northern areas (Tatar Strait) through the central banks (Yamato and Kitayamato rises) down south (around Oki Islands) were concordant. In all these regions, squid mature at a relatively small size (males are smaller than females) with modal classes of ready to spawn males of 160-170 mm DML and females of about 190 mm DML. Individuals larger than 220 mm DML were only females, and accounted for less than 1% of all analyzed sub-adult and adult squid. Everywhere in the Japan Sea, there is evidently only one rather extended spawning period for *B. magister* occurring during winter and spring, and peaks of spawning may differ from region to region. The existence of one generation of squid per year is evidenced by generally unimodal (for combined male and female data) size structure of adult squid almost everywhere in the Japan Sea.

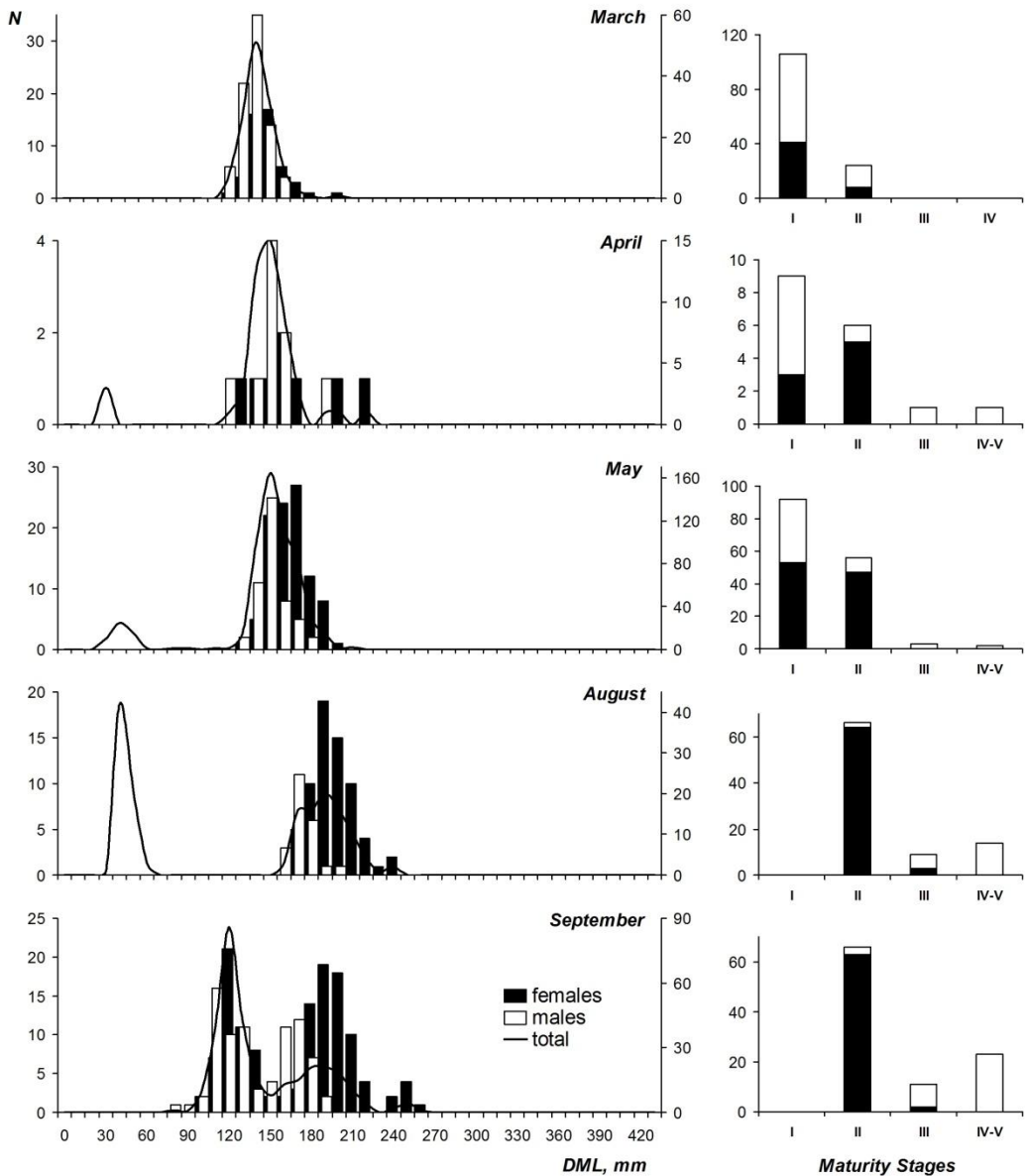


Figure 5. Size and maturity of *Berryteuthis magister* in the northern Japan Sea (Tatar Strait).

In some cases, however, the presence of additional peak of small squid in autumn (in the Tatar Strait and Kitayamato Bank) may indicate that these animals will probably be spawning later in spring or even in the early summer. Large body of data on *B. magister* aggregations collected in the Pacific Ocean off the Kuril Chain, off Kamchatka and in the western Bering Sea suggests that, in all research areas, squid of various sizes and maturity were present throughout the entire year, and there was no clear pattern in monthly progression of size for the regionally pooled data; however, there were some geographic and seasonal variations in maturity patterns, which may indicate the existence of temporal inconsistency in size-and-maturity structure of the squid aggregations (Figures 9-14).

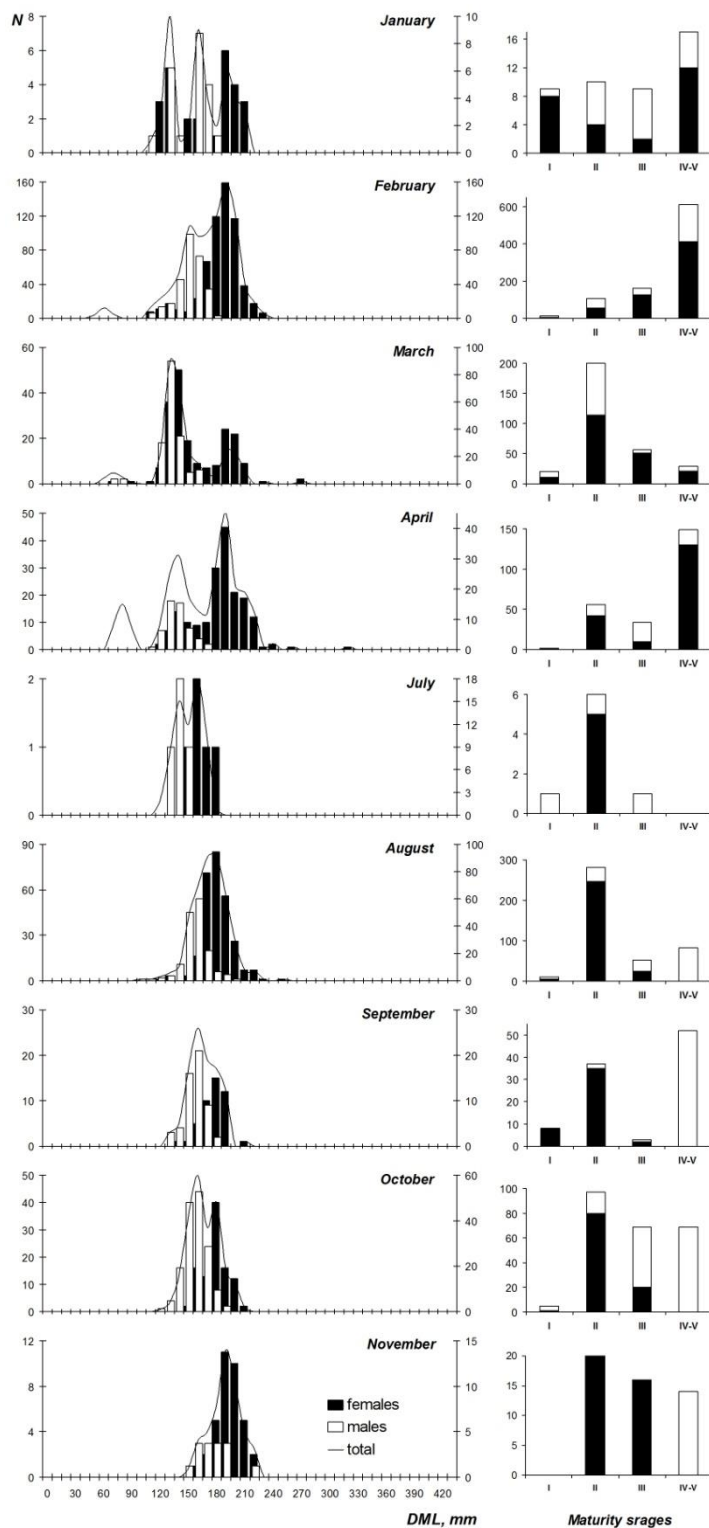


Figure 6. Size and maturity of *Berryteuthis magister* in the central Japan Sea (underwater rises).

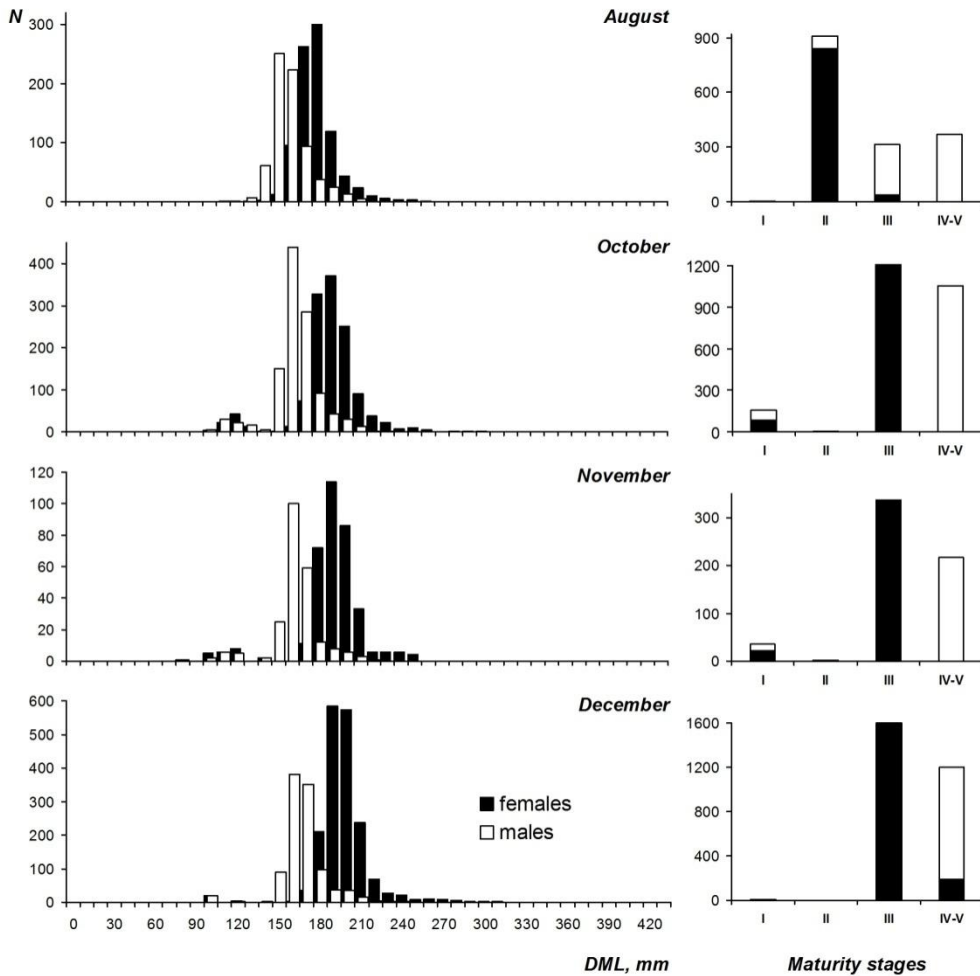


Figure 7. Size and maturity of *Berryteuthis magister* on the Kitayamato Bank.

In all areas, squid size (DML) ranged from about 30 to 300 mm, being larger only occasionally. Early juvenile squid with DMLs 30-60 mm appeared only occasionally in trawl catches, and mainly in spring and autumn. In some areas, there were evident monthly shifts in the size of adult squid, e.g., modal DML classes of males and females increased progressively from March to May and from June to September off the south Kuril Islands, from October to December and from February to April off the northern Kuril Islands, from February to March and from April to September in the northwestern Bering Sea. However, in some areas suchlike changes were masked by the multi-generation complexity of squid aggregations, e.g. off the central Kuril Islands, in waters around the Commander Islands. In some cases data were restricted to get a reasonable pattern of monthly size progression, e.g. in Pacific waters off eastern Kamchatka. Size structure analysis of *B. magister* aggregations, coupled with data on maturity and age, revealed that in fact, there exist at least two successive generations in this species in the northern Bering Sea (Bizikov, 1996; Bizikov, Arkhipkin, 1996). The existence of at least two successive seasonal groupings of *B. magister* has also been suggested for the squid inhabiting the slope off the Kuril Chain (Fedorets et al., 1997; Fedorets, 2006).

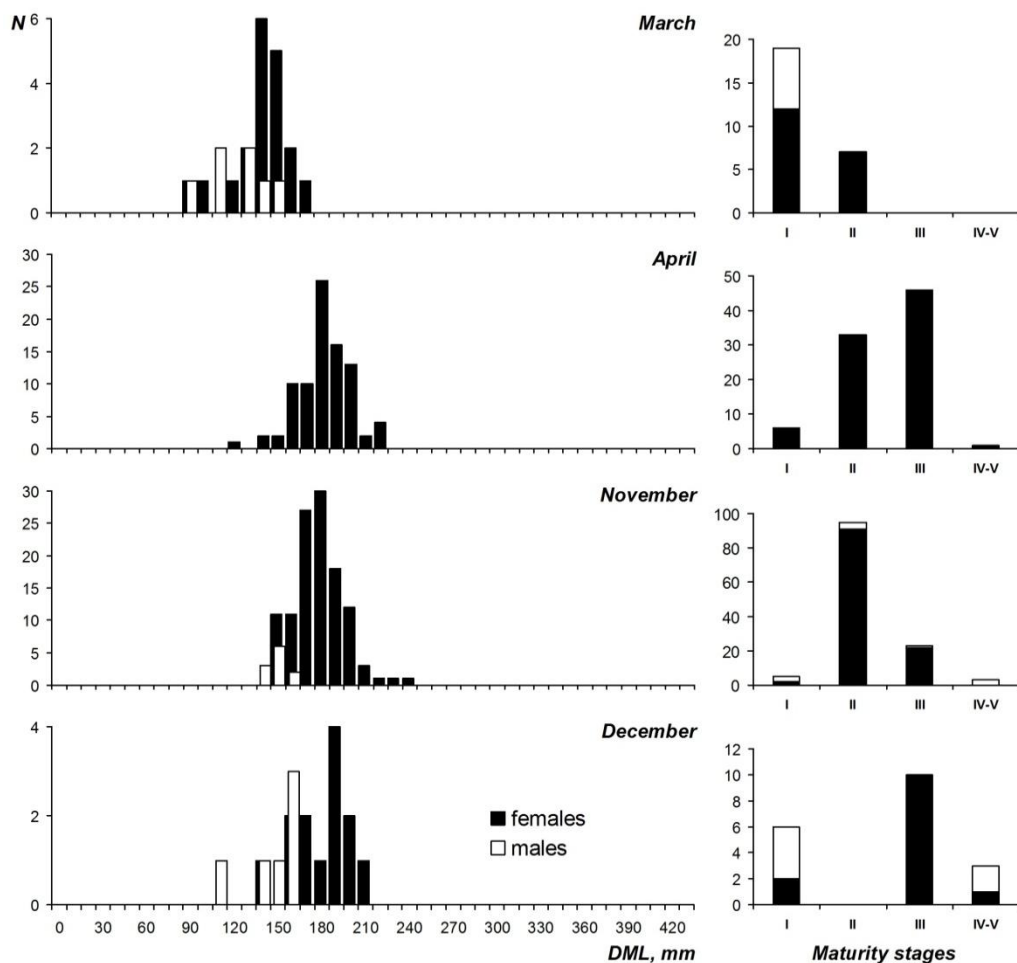


Figure 8. Size and maturity of *Berryteuthis magister* in the southwestern Japan Sea (around Oki Islands).

Our data on the squid maturity coupled with data on size made it possible to further corroborate the idea of the existence of successive seasonal generations in *B. magister*, at least in the northwest Pacific. Off the Kuril Islands, most squid in aggregations were immature (stages I and II) almost throughout the year, while in the Bering Sea, mature squid (stages III and higher) dominated all the year round with much clearer monthly variability in maturity patterns. In that respect, squid aggregations off eastern Kamchatka resembled those off the Kurils, and aggregations from banks around the Commander Islands resembled those of the western Bering Sea. Off the Kuril Islands, ready-to-spawn and spawning *B. magister* (stages V and higher) appeared twice a year: in spring and in autumn, – with some variability among the regions. In the northwestern Bering Sea, the pattern appeared rather similar: the highest proportions of spawning squid were registered in spring and autumn, while summer and winter months were dominated by immature and gaining maturity individuals. Taking into account *B. magister* size-and-maturity patterns, we may suggest that, in the Northwest Pacific, successive generations of this species spawn during greater part of the year with peaks in late spring and autumn.

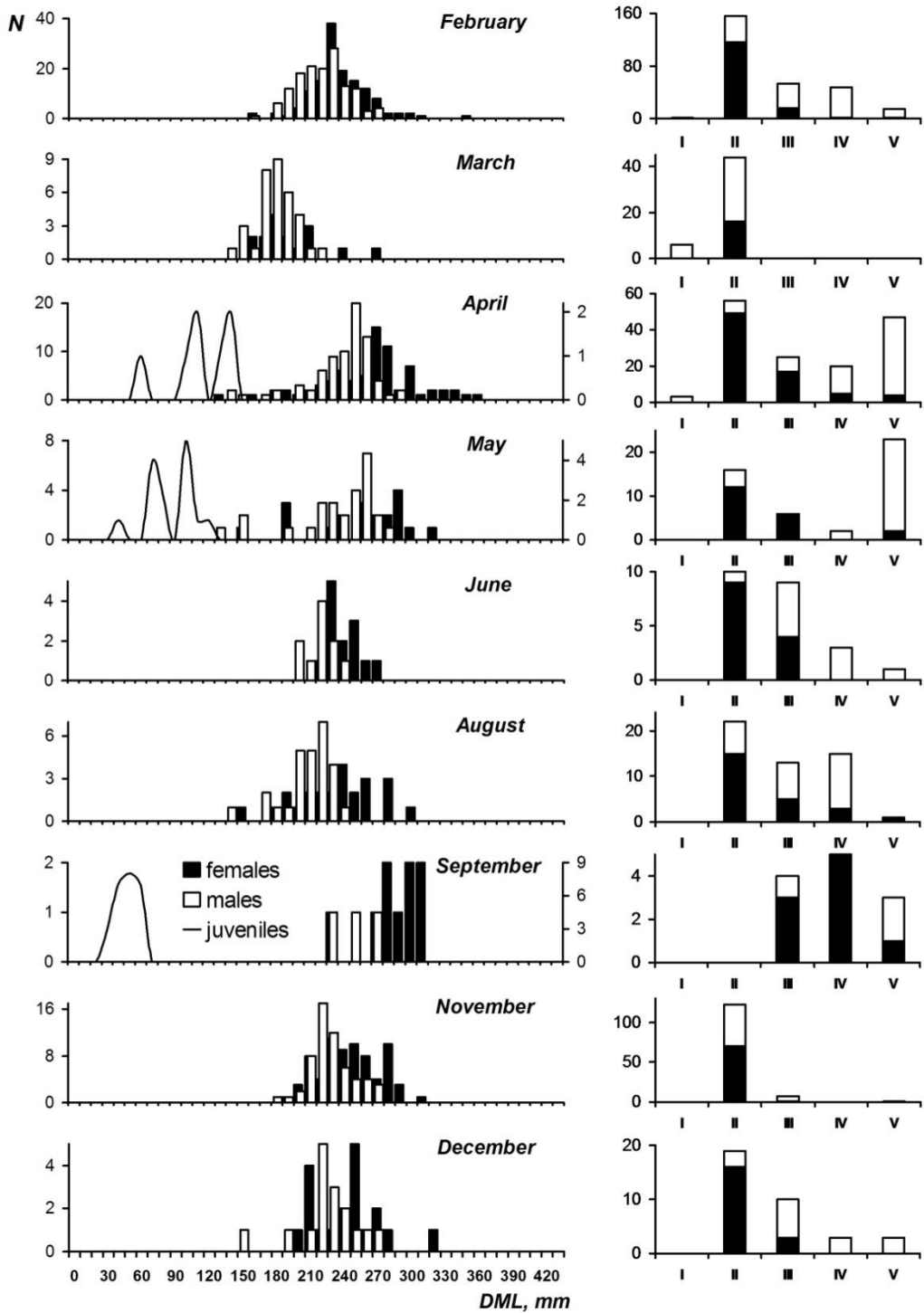
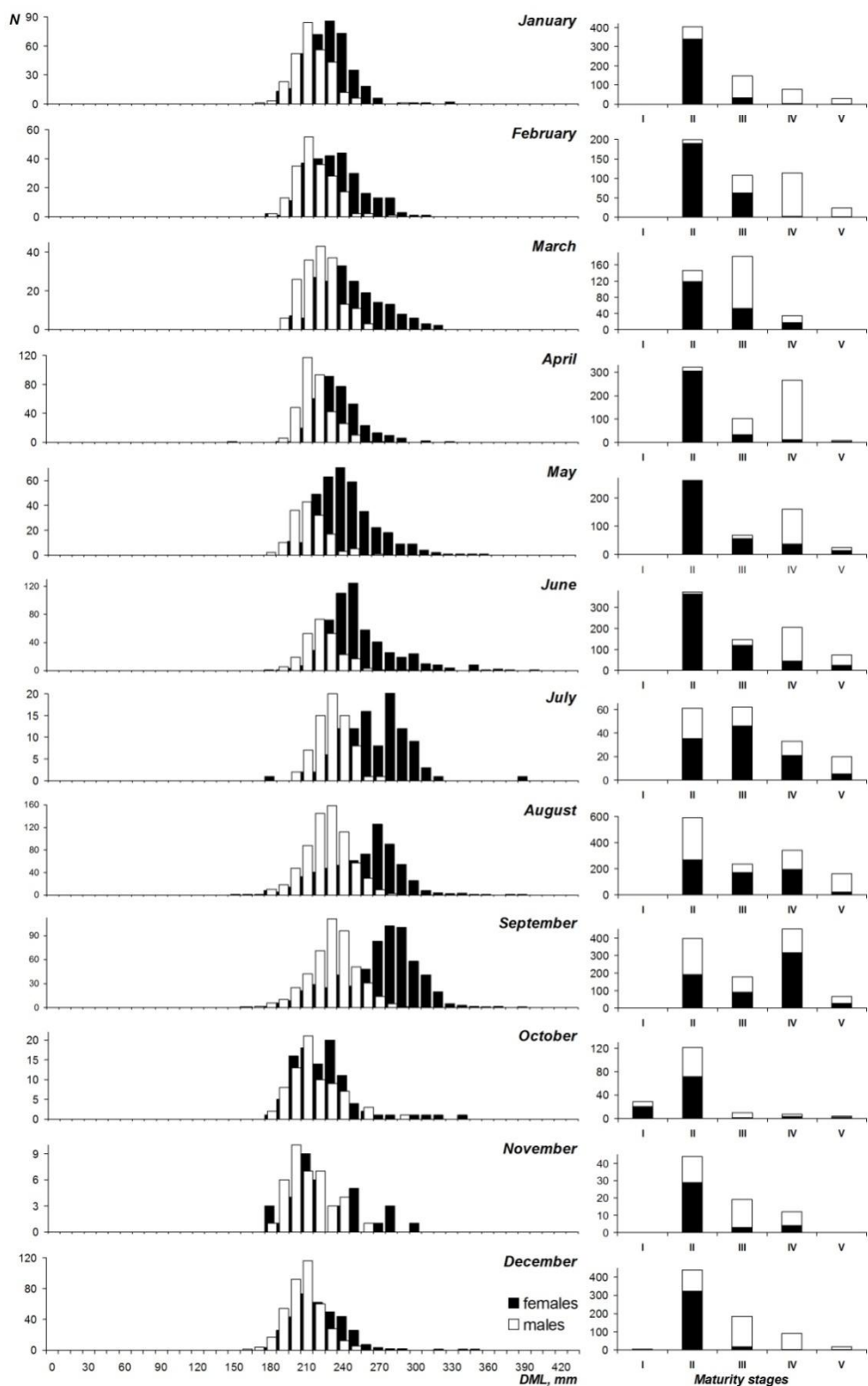


Figure 9. Size and maturity of *Berryteuthis magister* in the Pacific Ocean off south Kuril Islands.

Figure 10. Size and maturity of *Berryteuthis magister* in the Pacific Ocean off central Kuril Islands.

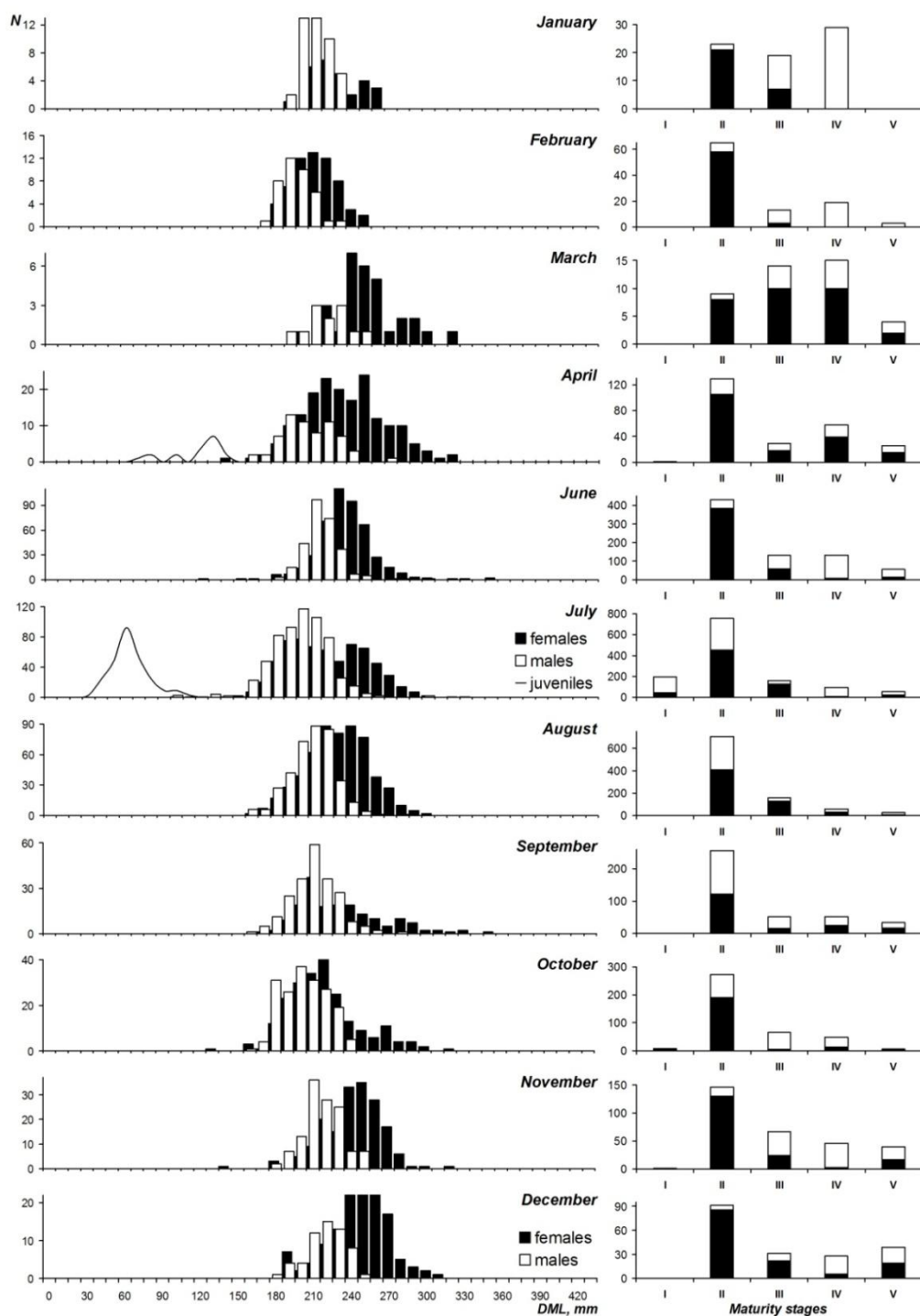


Figure 11. Size and maturity of *Berryteuthis magister* in the Pacific Ocean off north Kuril Islands.

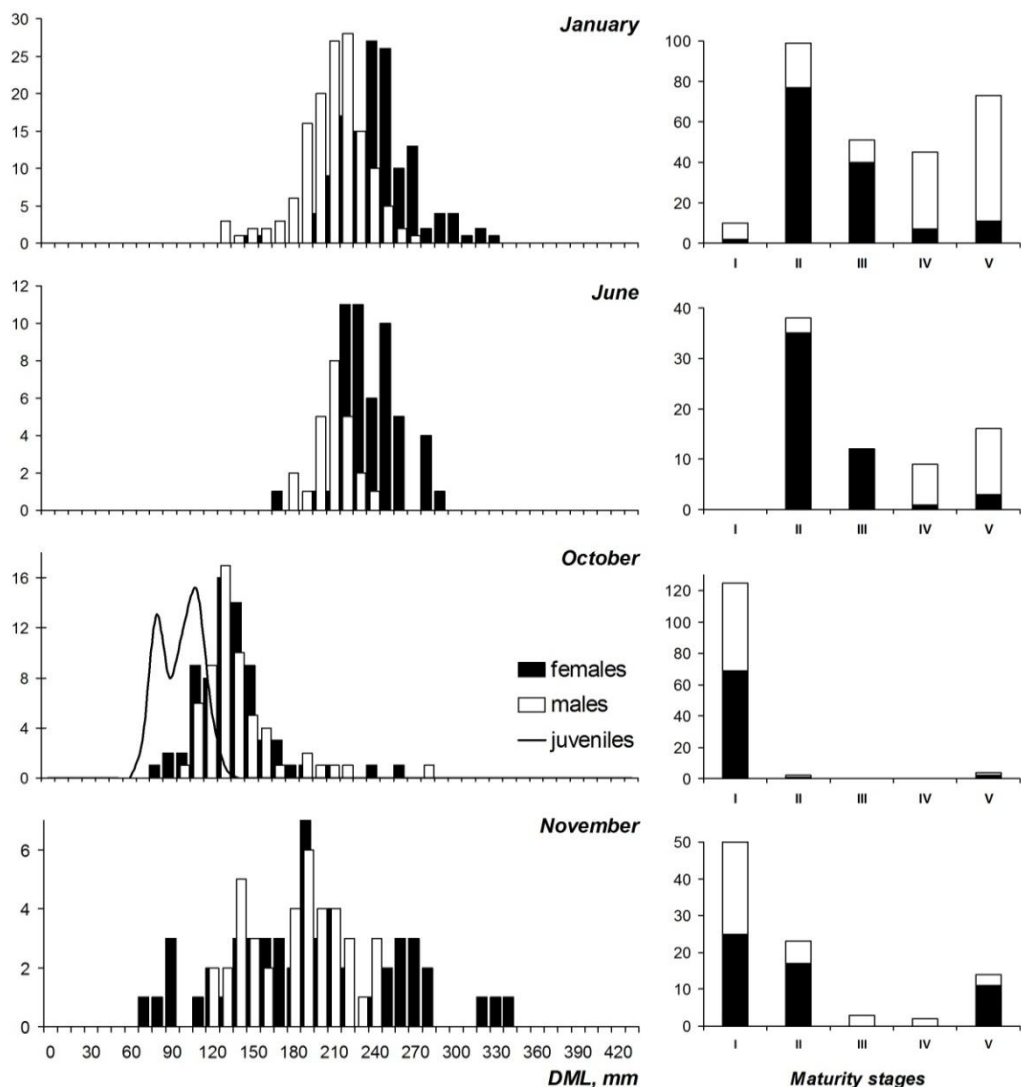


Figure 12. Size and maturity of *Berryteuthis magister* off eastern Kamchatka.

This is contrary to what we have observed in the Japan Sea, where *B. magister* spawn in winter and early spring, and spawning season is much less protracted than in the Northwest Pacific areas.

Our data on *B. magister* from the Northeast Pacific and southeastern Bering Sea are rather scarce compared to analogous data from the Northwest Pacific. However, these data also indicate that there exists monthly progression in the squid size (DML) and distribution of maturity stages, at least in the northern Gulf of Alaska and southeastern Bering Sea (Figure 15).

Interestingly, June patterns of size and maturity for individuals from the eastern Aleutian Islands appeared intermediate between June patterns for squid from the northern Gulf of Alaska and southeastern Bering Sea, which may indicate relatedness of squid from these areas.

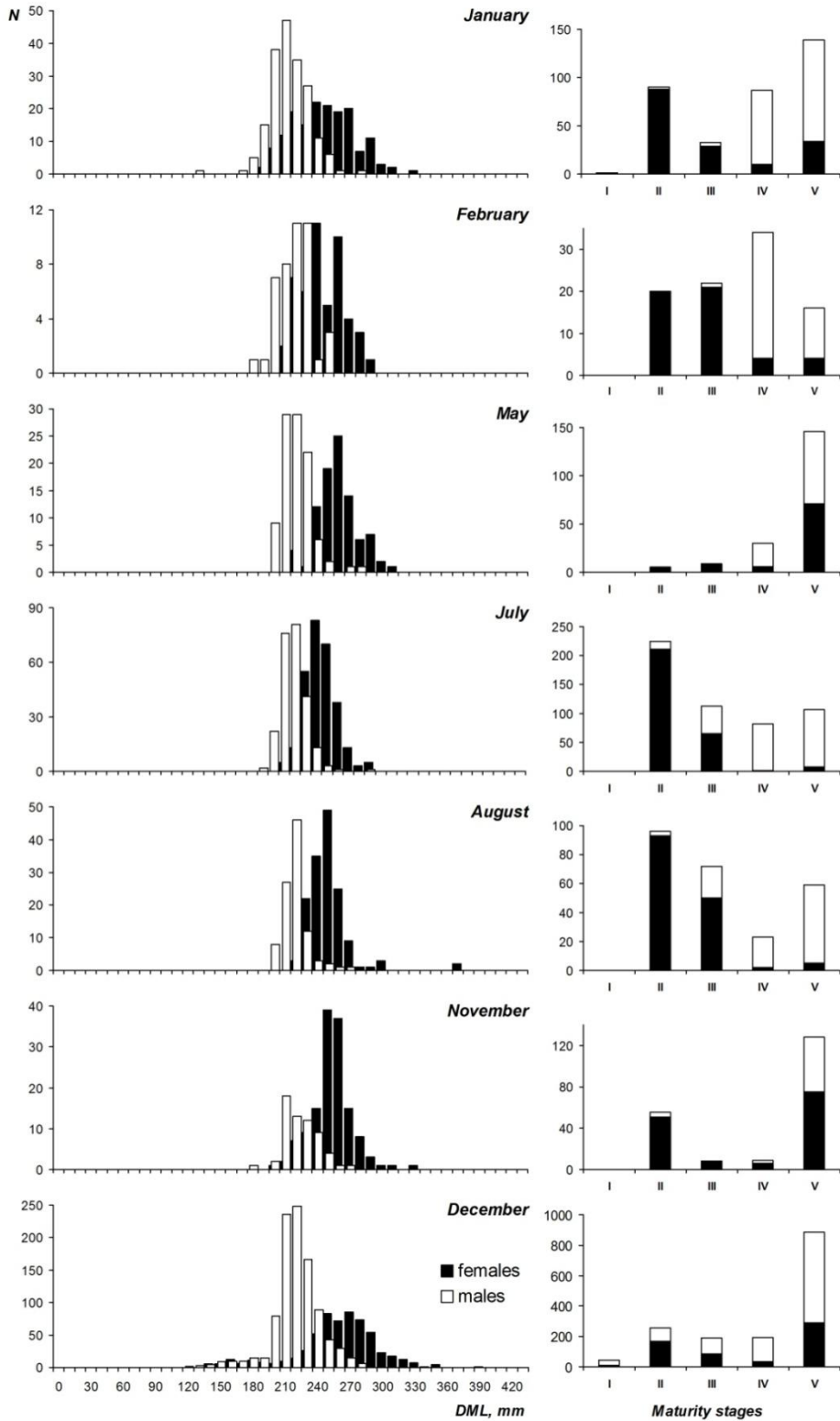


Figure 13. Size and maturity of *Berryteuthis magister* near the Commander Islands.

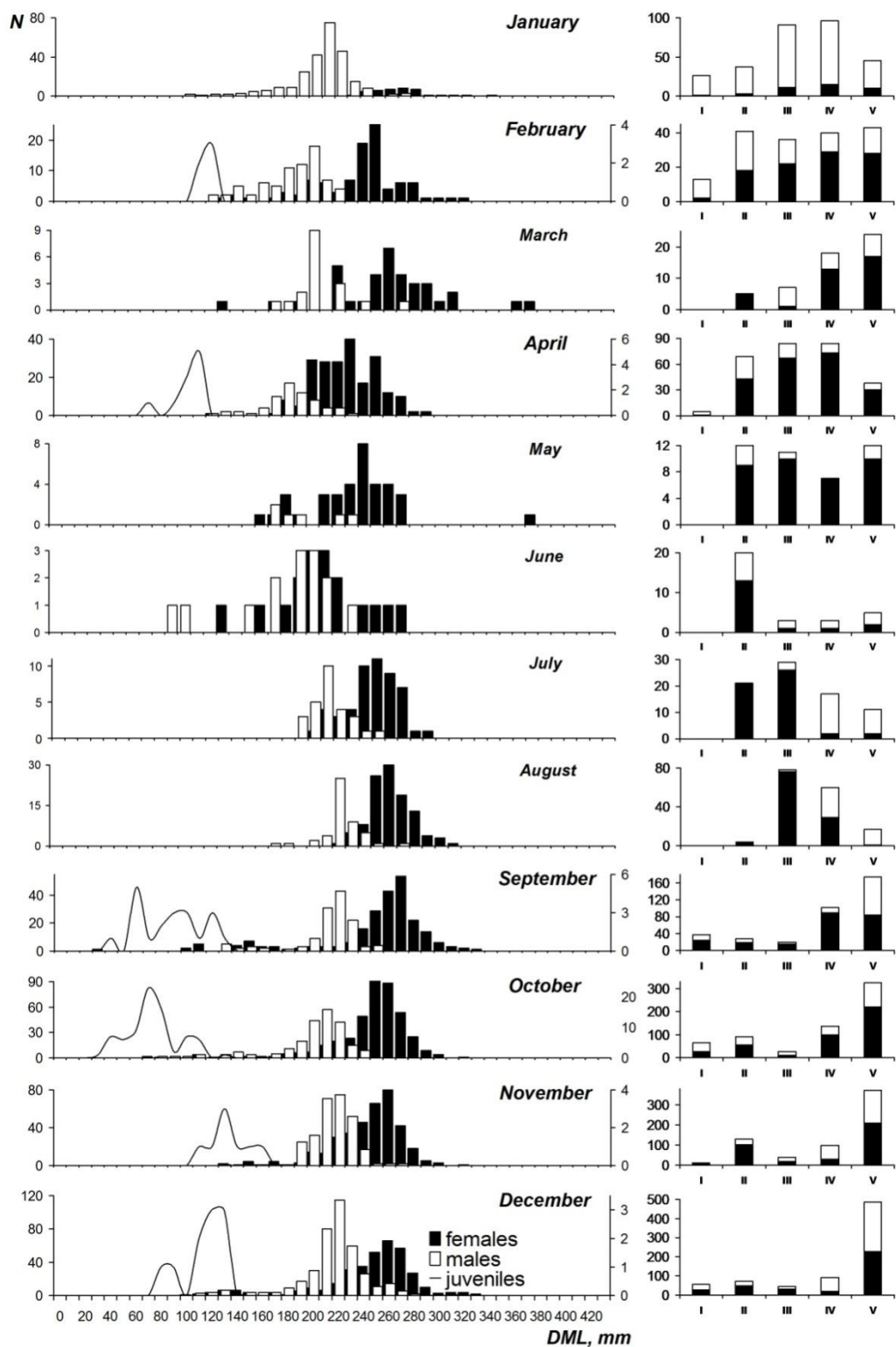


Figure 14. Size and maturity of *Berryteuthis magister* in the northwestern Bering Sea (left axis – adults, right axis – juveniles).

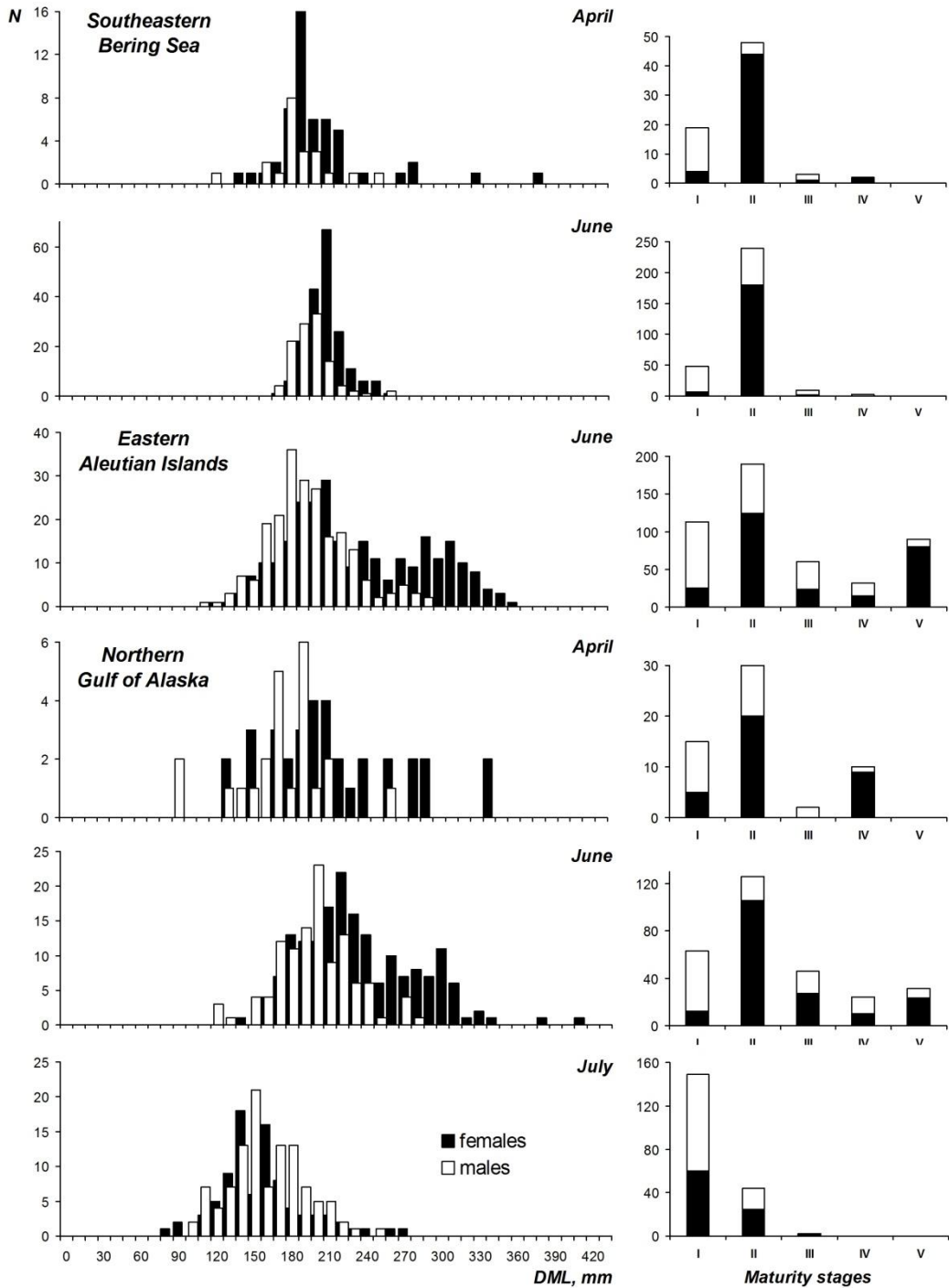


Figure 15. Size and maturity of *Berryteuthis magister* in the southeastern Bering Sea and northeastern Pacific Ocean (off eastern Aleutian Islands and in northern Gulf of Alaska).

Like squid aggregations inhabiting the Northwest Pacific, squid aggregations from the Northeast Pacific are composed of individuals with a wide size range, which may indicate that successive seasonal generations also occur in the eastern areas of the species range. This is contrary to the size-and-maturity patterns, which were revealed for the squid inhabiting the Japan Sea, where aggregations of the small-sized *B. magister* are more homogeneous and there is no clear evidence for the existence of seasonal successive groupings.

3.3. Feeding Behavior

Berryteuthis magister is an opportunistic hunter and, since this is one of the most abundant cephalopod species in the boreal demersal slope nektonic communities in the North Pacific Ocean and adjacent marginal seas, its role in the food webs is hard to overestimate. Numerous studies of *B. magister* feeding habits suggest that prey spectrum and feeding intensity depends upon the squid ontogenetic stage, time of the day and season, and is associated with migration activity, in particular, with vertical forage movements from near-bottom to upper layers, which are most clear at early life stages.

Small young squid consume mainly small planktonic organisms, and as they grow and tend to be less active in terms of vertical migrations, fish and squid occur more frequently in the diet of *B. magister*, though large planktonic and demersal crustaceans, e.g. Euphausiacea (*Thysanoessa* spp.), Amphipoda (*Themisto* spp., *Hyperia galba*) and Decapoda (*Pandalus* spp.), continue to play an important role as prey organisms (Chuchukalo, 2006; Fedorets, 1986; Fedorets, Kun, 1988; Gorbatenko et al., 1995, 2003; Kuznetsova, 1998, 2004; Kuznetsova, Fedorets, 1987; Nesic, 1989).

The analysis of database on *B. magister* feeding habits in the East Asian marginal seas suggested that there exists a seasonal pattern in foraging activity. In the Okhotsk Sea, squid feeding was less intensive in winter, when daily ration (=food consumption) accounted for only about 1% of the body weight for both young and adult squid (Table 2), and was notably higher in autumn and summer, when daily ration of foraging juveniles and immature adults accounted for about 4% of the body weight.

Similar patterns were observed in the northwestern Bering Sea slope in summer and autumn: adult and mature squid consumed daily relatively small amount of food (of about 1% of their body weight), while young and fast-growing *B. magister* consumed much more food daily (of about 4% of their body weight) (Chuchukalo, 2006).

In the Okhotsk and Bering seas, highly active and vertically migrating juveniles preyed mainly upon planktonic crustaceans (euphausiids and amphipods), and large demersal adult squid consumed larger prey: mainly mesopelagic fish (Myctophidae) and cephalopods (young *B. magister*), and occasionally shrimp (*Pandalus* spp.). On the yearly scale, different prey organisms accounted various portions of the squid diet, which could be due to different availability of these animals for squid (e.g., because of different changes in their abundances). As the squid mature, feeding intensity of *B. magister* decreases significantly, and prespawning and spawning squid do not take food at all.

Studies on daily foraging rhythm of adult *B. magister* on the slope off the Kuril Islands (as indicated by stomach fullness indices and digestion rate of food in stomachs during 24 hours of observations) revealed that feeding activity was the highest during daylight hours (in particular, at noon) and lowest during dark hours (in particular, at midnight) (Table 3).

Table 2. *Berryteuthis magister* diet in the Okhotsk Sea in winter (proportion of each food component in stomach contents is given in %) (from Chuchukalo, 2006)

Prey organisms	Juveniles (DML 70-110 mm)		Adults (DML 120-220 mm)	
	Depth range, m			
	0-200	200-500	0-500	200-500
Euphausiacea	46.6	43.6	46.1	13
<i>Thysanoessa longipes</i>	35.7	41.1	36.6	13
<i>T. raschii</i>	8.8	2.5	7.7	-
<i>Thysanoessa</i> spp.	2.1	-	1.6	-
Copepoda	+	2.4	0.4	0.3
<i>Pareuchaeta japonica</i>	+	0.6	0.1	0.3
<i>Metridia pacifica</i>	-	+	+	-
<i>Neocalanus cristatus</i>	-	0.6	0.1	-
Amphipoda	46.9	12.8	41	2.3
<i>Themisto japonica</i>	45.8	10.3	39.6	1.7
<i>Primno macropa</i>	1.1	2.5	1.3	0.6
Coelenterata (unidentified)	2.2	2.2	2.2	-
Chaetognatha	-	2.2	0.4	-
<i>Parasagitta elegans</i>	-	2.2	0.4	-
Osteichthyes	0.3	25.9	4.7	68
<i>Leuroglossus</i> sp.	-	13.3	2.4	46.5
<i>Stenobrachius</i> sp.	-	-	-	1.5
Osteichthyes (unidentified)	0.3	12.2	2.3	20
Teuthida (unidentified)	4	10.9	5.2	16.4
Time of observations	22:00-05:00	24 hours	24 hours	24 hours
Number of squid analyzed	71	85	156	69
Daily consumed food (% of the squid body weight)	1	0.8	1	-

These observations suggest that large squid “wait” for their major prey (planktonic crustaceans) to settle down to near-bottom layers during the day, and do not follow forage organisms at night when they ascend to midwater and subsurface layers. At night, when crustaceans swarmed the pelagic zone, adult squid hunted occasionally upon fish and cephalopods (smaller *B. magister*). Young squid, which relatively frequently occur in the mesopelagic zone, present somewhat different pattern of feeding activity. In the mesopelagic Okhotsk Sea, for example, squid with less than 110 mm mantle length foraged most actively at night (during 3-5 A.M.) and in the afternoon (during 2-6 P.M.). These observations indicate that juvenile squid may follow their planktonic prey in the water column.

3.4. Predators and Parasites

Numerous pelagic and demersal marine species prey upon *B. magister* in the North Pacific. Among these are seabirds, e.g., thick-billed murre (*Uria lomvia*) and marine mammals, e.g., northern fur seal (*Callorhinus ursinus*), Steller sea lion (*Eumetopias jubatus*),

Dall' porpoise (*Phocoenoides dalli*), Baird's beaked whale (*Berardius bairdi*), short-finned pilot whale (*Globicephala macrorhynchus*), sperm whale (*Physeter macrocephalus*); the squid is preyed upon by bottom skates (*Bathyraja* sp.), as well as various pelagic and demersal bony fish: Pacific salmon species (*Oncorhynchus* spp.), Pacific halibut (*Hippoglossus stenolepis*), Greenland turbot (*Reinhardtius hippoglossoides*), arrowtooth halibut (*Atheresthes* spp.), sablefish (*Anoplopoma fimbria*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), grenadiers (*Albatrossia pectoralis*, *Coryphaenoides armatus*, *C. filifer*), threadfin hakeling (*Laemonema longipes*), deep-sea rockfishes (*Sebastes borealis*, *S. aleutianus*, *S. alutus*, *Sebastolobus macrochir*, and *S. alaskanus*), sculpins (*Malacocottus zonurus*), snailfishes (*Polypera simushirae*), eelpouts (*Lycodes soldatovi*, *L. brevicaudatus*, *Bothrocara brunnea*, *B. hollandi*); cephalopods also consume this squid, e.g. larger individuals of *B. magister* may hunt upon smaller ones (Chuchukalo, 2006; Nesis, 1998; Okutani et al., 1988; Percy, Ambler, 1974), and it was found in stomach contents of *Todarodes pacificus* in the Japan Sea in summer (Mokrin N.M., pers. comm.).

Some species may prey heavily, or even almost exclusively upon *B. magister* in certain areas and times, suggesting that they choose the squid purposefully. For example, our observations (unpublished data) revealed that, on the slope off the Kuril Chain, giant squids, e.g., robust clubhook squid (*Onykia robusta*) and Makko gonate squid (*Boreoteuthis* cf. *makko*) prey exclusively upon adult *B. magister* in autumn; on the northwestern Bering Sea slope, Greenland turbot prey largely upon the adult squid, when these aggregate in autumn before spawning, and large-sized adult Chinook salmon (*Oncorhynchus tshawytscha*) feed almost exclusively on juvenile *B. magister* in the late autumn and winter. This squid is among the favorite prey species for the northern fur seal all over the North Pacific Rim, and accounts for up to 25.8% of this pinniped's diet in the Japan Sea (Panina, 1966, 1971).

Table 3. *Beryteuthis magister* daily feeding activity off the Simushir Island in spring (proportion of each food component in stomach contents is given in %) (from Chuchukalo, 2006)

Prey organisms	Time of the day, hours						24 hours
	0	4	8	12	16	20	
Plankton	+	21.5	11.2	88.7	100	100	75.4
Euphausiacea	+	21.5	11	87.6	95	81	71.8
Amphipoda	-	+	0.2	+	+	-	0.2
Calanoidea	+	+	+	0.8	5	19	3.1
Chaetognatha	-	-	-	0.3	+	+	0.3
Nekton	100	78.5	88.8	11.3	+	-	24.6
Osteichthyes	100	78.5	0.2	-	-	-	10.8
Teuthida	-	-	88.6	11.3	+	-	13.8
Average stomach fullness, % ⁰⁰	11.6	3.1	10.2	76.9	34.1	13	24.8
Number of squid analyzed	25	25	25	25	25	25	150
Empty stomachs, %	92	80	68	0	48	56	58

Various parasites were found in *B. magister*: unidentified ciliates; digenetic flukes (*Derogenes varicus*); tapeworms (*Phyllobothrium* sp. and *Nybelinia surmenicola*); acanthocephalans (*Echinorhynchus cotti*); anisakid nematodes (*Anisakis simplex* and *Hysterothylacium reliquens*); and protistans *incertae sedis* (*Hochbergia* sp.) (Avdeyeva et al., 1982; Bagrov, 1982; Hochberg, 1990; Kasahara et al., 1978; Nesis 1996). Usually, the rate of infection with parasites, e.g., tapeworms and nematodes, increases with squid age (Avdeyeva et al., 1982; Bagrov, 1982). The fauna of parasites in *B. magister* is similar to that in other oceanic squid, which are known to be intermediate, transport or reservoir hosts for parasites, also common in pelagic and demersal fish (Hochberg, 1990; Nesis, 1998).

3.5. Intraspecific Variation and Population Structure

Intraspecific variability and population structure of *B. magister* was analyzed using genetic and classical morphologic approach. Allozyme-coding genetic loci were thoroughly studied in *B. magister* from almost the entire species range, including numerous sites in the Japan, Okhotsk and Bering seas, northwestern Pacific Ocean off the Kuril Islands, around the Commander Islands, off the eastern Aleutians and in the Gulf of Alaska (Katugin, 1993a, 1995a, 1998, 1999, 2000, 2002).

These studies have revealed several important issues which should be considered in the analysis of the species population structure and life cycle patterns. First, it appeared that *B. magister* is unique among the Gonatidae in having the highest levels of genetic variation as revealed from multi-locus screening of allozymes. Of 42 protein-coding loci 24 appeared polymorphic, and average observed heterozygosity H_{ob} ranged from 0.104-0.137, which suggested a high potential for differentiation. Indeed, further research has unraveled a geographic pattern in genetic composition of *B. magister* aggregations across the species range. Wide-scale approach using genetic distance and heterogeneity analyses showed that there exists a geographically-related subdivision of the species gene pool. Squid populations from the Japan Sea, Northwest and Northeast Pacific significantly differed from each other even at small number of loci (Figure 16).

Within the Northwest Pacific, squid living in the Okhotsk Sea and off the Kuril Chain were less different between each other than from the Bering Sea squid. The measure of genetic differentiation $F(ST)$ followed the pattern revealed using genetic distances, and was the highest between squid from the Japan Sea and other two macro-regions (0.009-0.013), somewhat lower between squid from the Northeast and Northwest Pacific (0.006) and the lowest between squid aggregations inhabiting the Northwest Pacific (0.001).

The use of additional polymorphic loci yielded a more detailed pattern of genetic differentiation for *B. magister*. Squid from the Japan Sea appeared very different from squid occurring off the Kuril Islands at 7 of 12 polymorphic loci (for a total of 26 gene loci used in the comparison) with mean $F(ST)$ value as high as 0.12, which was 10 times higher compared to the $F(ST)$ value from small number of loci.

Total level of genetic divergence between squid occurring along the Kuril Islands and in the western Bering Sea remained relatively low for comparisons using 4, 7 and 10 highly polymorphic loci: $F(ST)$ ranged from only 0.001-0.002. Genetic distance tree branch topography suggested the existence of at least two major geographic squid groups: Okhotsk-Kuril and Bering, – which were clearly different from each other.

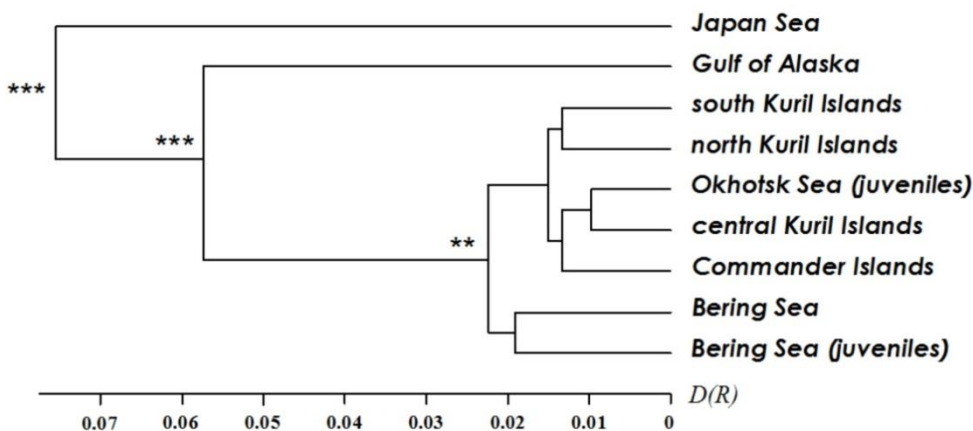


Figure 16. Dendrogram of Rogers' (1972) genetic distance $D(R)$ for *Berryteuthis magister* from different regions of the species range (asterisks at the nodes indicate probability for heterogeneity among squid samples: ** - $P < 0.1$; *** - $P < 0.01$).

The first group included squid from the Okhotsk Sea and the Pacific Ocean off the central and north Kurils, and the second one – squid from the northwestern Bering Sea. There was no genetic heterogeneity within each group. South Kuril squid differed from their closest neighbors at 2 of 7 polymorphic loci. Squid from the banks near Commander Islands slightly (but statistically significantly) differed from the Okhotsk-Kuril squid at 1 of 7 loci, and from Bering squid at 1 of 7 loci. The use of hierarchical analysis of standardized variance (F) in allele frequencies revealed that 76% of genetic variability among the squid collections were attributable to differences between the groups, which is a good support for the observed clustering, implying that such a grouping reflects the existence of population structure among aggregations of *B. magister* in the Northwest Pacific.

Individuals of *B. magister* from various regions of the species range showed some differences in size, in particular, when dorsal mantle length was plotted against nidamental gland length in females; however, the use of general size was able to reveal clear differences only between notably smaller squid from the Japan Sea and much larger squid from other parts of the species range (Katugin, 1998, 2000). More detailed pattern was obtained, when variability in morphological traits of *B. magister* was analyzed using external parameters of the gladius (Katugin et al., 2004). Although the teuthid gladius has been widely used in systematic and evolutionary studies (Bizikov, 1996, 2008; Toll, 1998) its value as a character for population studies of squid is yet to be estimated.

Not to introduce possible age-related differences in gladius shape, gladii were sampled only from adult *B. magister* from the Japan Sea, northern Okhotsk Sea, off the north Kuril Islands in the Pacific Ocean, off eastern Kamchatka in the Pacific Ocean, the western Bering Sea (Olutorskyi Bay), the northern Bering Sea (off Cape Navarin) and off Vancouver Island in the Pacific Ocean. The following 8 standard measurements of each gladius were taken: gladius length (GL), gladius width (GW), free rachis length (RL), free rachis width anterior (RW), conus field length (FL), conus field width (FW), conus length (CL), and conus width (CW). Gladius dimensions were then adjusted relative to GL, and the following 7 indices were calculated for every gladius: GW/GL , RL/GL , RW/GL , FL/GL , FW/GL , CL/GL , and CW/GL .

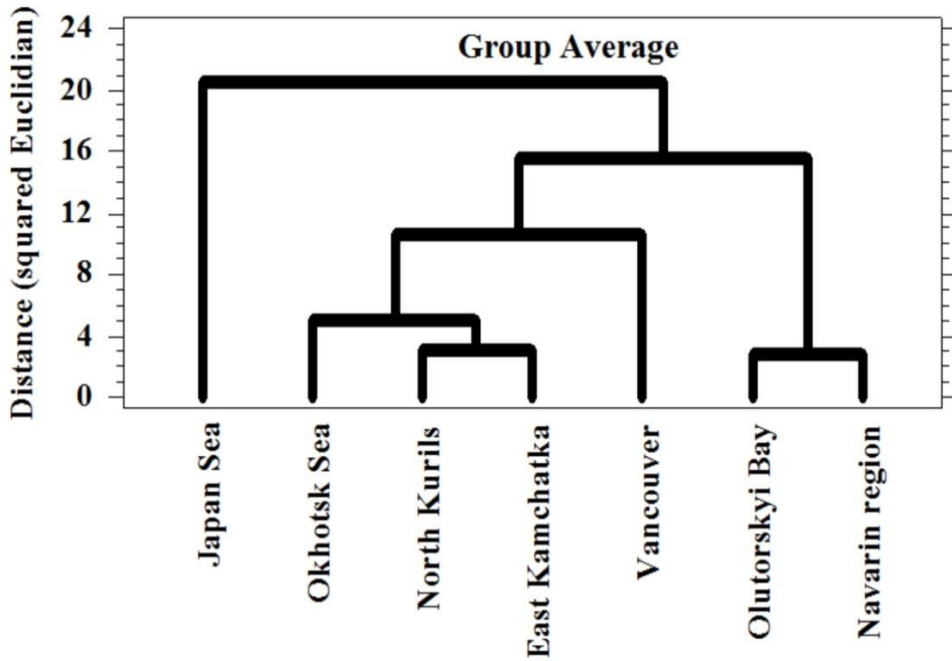


Figure 17. Cluster analysis of gladius indices for *Berryteuthis magister* from different regions.

Results from cluster analysis of mean gladius indices (based on the squared Euclidian distance matrix, produced using the group average method) suggested a geographically structured pattern of variability among squid samples from different regions (Figure 17). Principal component analysis (the first two components that together accounted for 76.1% of the variability) also revealed a strong geographic pattern of gladius variability among samples and was similar to the grouping obtained from cluster analysis, showing separation of the Japan Sea and Northeast Pacific squid from the others, and two Northwest Pacific assemblages: the northwestern Bering Sea group (from Olutorskyy Bay and Navarin region) and a group that includes squid from the Okhotsk Sea, off the north Kurils and east Kamchatka. Both genetic and morphometric studies suggested that there exists inconsistency in distributions of strictly hereditary (allele frequencies at structural genes) and epigenetic (form of the gladius) characters for *B. magister* from different parts of the species geographic range. Moreover, there was a striking similarity in the outcomes from the studies using independent sets of characters, and that concordance clearly indicated that there exists intraspecific structure in *B. magister*. First, squid from the Japan Sea are significantly different from squid inhabiting other regions of the North Pacific, and previous analysis of various data sources unequivocally suggested that the squid populations living in that semi-isolated water body have evolved into a separate subspecies (Katguin, 2000). Second, *B. magister* populations from the Gulf of Alaska and adjacent waters off eastern Aleutians differ from conspecific populations inhabiting the Northwest Pacific. And third, the squid aggregations living in the latter area can also be distinguished from each other in genetics and morphology. In particular, squid inhabiting the northwestern Bering Sea differ from squid living in the Okhotsk Sea and along Kuril Islands, while squid from the latter two areas are much closer to each other.

One curious outcome from allozyme and morphometric studies is that squid occurring near the Commander Islands and on the Pacific Ocean slope off neighboring East Kamchatka appeared to be closer to the Okhotsk-Kuril group than to the northwestern Bering Sea group, which in fact is not surprising given the existing pattern of water transport in those regions.

The revealed patterns of intraspecific variability provided deeper insight into *B. magister* population structure, which appeared to be geographically related. Isolated and semi-isolated population systems, which exist across the extended species range, exhibit a classical mode of geographic speciation, when populations in the Japan Sea evolved into a separate subspecies with unique genetic and morpho-ecological characters, and populations from other North Pacific areas fit into isolation-by-distance scenario, and less differ from each other in genetic and morphological traits, but acquired region-specific patterns in ecology (Katugin, 2002).

3.6. Life Cycle

Both earlier proposed hypothetical schemes for *B. magister* life cycle are similar in many aspects (Kubodera, 1982; Fedorets, 2006). In particular, the authors suggested that, immediately after hatch deep on the slope, squid paralarvae ascend to the sub-surface layer and lead a relatively long planktonic life in the upper column until the beginning of ontogenetic descend.

However, since there are practically no reliable records of paralarvae from the upper epipelagic zone, and, taking into consideration the existing reliable information on the squid spawning behavior, egg-masses, occurrence of early life stages, juveniles and adults (see above, 2.1), we propose a modified version of the species life cycle, taking autumn-spawning generation as an example (Figure 18).

In the late autumn, large spherical egg-masses are deposited by females on the bottom, usually deep on the slope. Embryonic period lasts several months (half a year or even longer), and paralarvae with mantle length of about 3-4 mm hatch in the early summer.

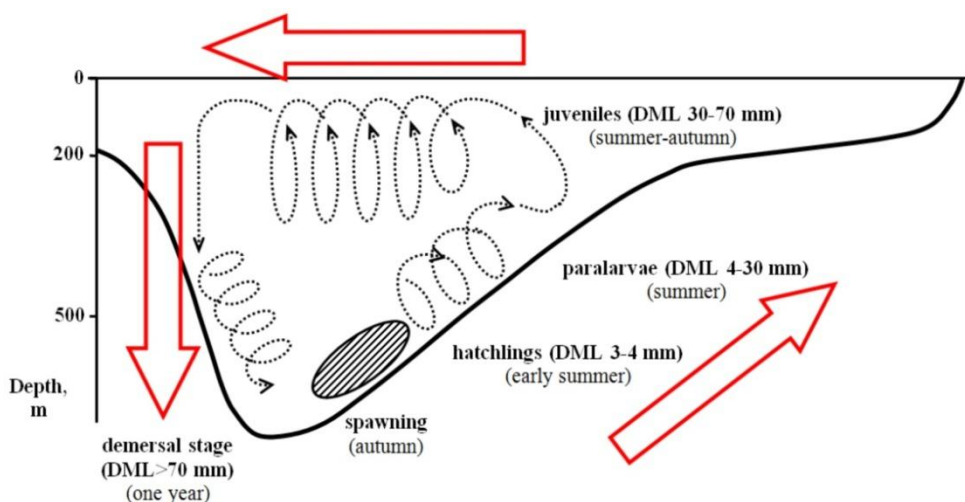


Figure 18. Generalized scheme of *Berryteuthis magister* life cycle (DML – dorsal mantle length).

Newly hatched paralarvae remain near the bottom for about a month until they grow to about 20-30 mm in mantle length, when, in the peak of summer, they start diel vertical forage migrations between meso- and epipelagic layers. Such a phase lasts about three – four months until young squid grow to about 50-70 mm in mantle length, and in autumn they start predominantly demersal life near the bottom. The absence of purely epipelagic phase and, therefore, restricted susceptibility to dispersal by surface currents at early stages, is in line with observations that, in *B. magister*, nursery, forage and spawning grounds are not clearly separated geographically. As they grow and mature, squid continue forage migrations; however, they usually do not visit upper layers, and conduct forage movements along the slope and occasionally into the mesopelagic zone. Demersal life lasts about one year until death after spawning. Having reached definitive size (males at about 210-230 mm and females at 260-280 mm mantle length) and having gained sexual maturity, squid start to mate. Mating occurs in autumn immediately prior to spawning, and squid can mate and spawn several times (females up to three times). Therefore, in *B. magister*, life cycle duration is about two years, of which an embryonic period lasts about six months, and the rest is due to postembryonic phase.

4. Fisheries

4.1. Stock Structure

In the Okhotsk and Bering seas and adjacent oceanic areas, the observed dynamics in development, existence and disappearance of commercially fished aggregations of *B. magister* is associated with seasonal patterns in the squid distribution, which reflects specific life cycle patterns and associated stock structure. Distribution density of the squid commercial aggregations and catch per unit effort (CPUE) are clearly increasing in the beginning of mass maturation and spawning. A rise in the proportion of mature individuals in commercial aggregations of the squid twice a year suggests that there exist successive generations, which according to the time of their mass occurrence at the fishing grounds, were called spring-summer and autumn-winter (Fedorets et al., 1997; Railko, 1983). Seasonal spawning aggregations are usually formed during approximately three months, and spawning of both seasonal generations lasts 1.5-2, up to 2.5 months, which means that commercial harvest of the species may last up to eight-nine months every year. Off the Kuril Islands, these generations are easily distinguishable in years, when the squid catches (and abundance) are close to the long-term average value, and an apparent decrease in abundance occurs in the mid-summer (from July to mid-August) and winter-spring (from December to March). However, in years of high abundance, both major waves of abundance corresponding to two successive generations significantly overlap, and therefore seasonal catch drops are not as clear as usual.

In the northwestern Bering Sea, the analysis of *B. magister* stock structure, based on size and maturity coupled with ageing of the squid using statoliths, yielded similar results (Arkhipkin et al., 1996; Bizikov, Arkhipkin, 1996). Individuals of two seasonal cohorts (which originated from spring-summer and autumn-winter spawning events) comprise the squid stock, which is harvested by commercial fishery.

Squid that belong to the spring-summer cohort are relatively low abundant and spawn from May through July and occasionally August. Squid of the autumn-winter cohort are highly abundant, larger than their counterparts, comprise the bulk of the Bering Sea stock and spawn from the late October through December and further until March.

4.2. Landings

Commercial harvest for *B. magister* is based on relatively large maturing and mature individuals, which aggregate near the bottom, and rarely occur in the meso- and epipelagic layers. Most of commercial catch is taken using bottom trawls, and lesser amounts of squid are taken as bycatch using mesopelagic trawl nets towed near the bottom, e.g. during fishery for walleye pollock and other demersal fish on the outer shelf and continental slope. Catch fluctuations of *B. magister* have been observed during pelagic and bottom research surveys and observations during specialized commercial bottom trawl fishery for this species by Russian research and commercial vessels in the northwestern Pacific Ocean off the Kuril Islands and southeastern Kamchatka, and in the northwestern Bering Sea. In these areas, total catch for *B. magister* by Russian fishery peaked at 90.3 thousand metric tons in 2006.

The oceanic area adjacent to the north and central Kuril Islands appeared the most productive in terms of commercial harvest for *B. magister*. In the last decade, the total catch for this squid there varied from 38.3 to 76.7 thousand metric tons, normally comprising 80.6-99.3% of the total squid catch by Russian fishery, being the smallest, of 60.9%, in 2010, when the catch in the western Bering Sea peaked at its historical maximum of about 13.1 thousand metric tons. Usually, Bering Sea landing are about 10 times lower than landings off the Kuril Islands, which is mostly due to the fact that, in the former area, squid are taken as bycatch. Beginning from 2004, the upper slope fishing grounds to the east of southeastern Kamchatka became the second most productive area for the bottom squid fishery, with annual catches ranging from 8.4-10.6 thousand metric tons and comprising up to 17.7% of the total *B. magister* catch in the Russian Far Eastern seas. Much less squid were usually harvested in the western Bering Sea, where annual catch normally varied from 1.6 to 7.25 thousand tons, comprising 2.5-12% of the total catch for this species in the Russian EEZ. In the ocean off the south Kuril Islands, the squid annual catch ranged from 1.98-4.3 thousand tons in 2004-2007, which made up 2.6-5.1% of the total Russian catch for *B. magister*.

4.3. Stock Abundance

Distribution density and biomass assessments for *B. magister* were made not on a regular basis, and there were rather few research trawl surveys, which covered deep-sea slope regions with the typical squid habitat. Data collected in TINRO-Centre expeditions suggested that, in the Okhotsk Sea, the squid biomass in the pelagic zone way exceeds half a million tons in winter and spring, and may be several times higher in highly productive autumn season (Table 4). Within the Okhotsk Sea, the species is most abundant in the north beyond the shelf, where about 50-80% of the “total” biomass is distributed, and occurs primarily in the

Table 4. Distribution density (kg per square km) and biomass (thousand tons, in brackets) of *Berryteuthis magister* in the Okhotsk Sea (from Lapko (1996) and Fedorets (2006))

Region	month, year										
	II-IV 1990				VIII 1989	XI 1990 - I 1991				X-XII 1991	IX-XI 1994
	water layer										
	epi-	meso-	bathy-	Total pelagic	meso-	epi-	meso-	bathy-	Total pelagic	epi-	epi-
Northern	209 [13.1]	4,832 [302.5]	19 [1.2]	5,060 [316.8]	5,451 [1,166.5]	94 [33.0]	1,048 [367.0]	131 [0.8]	1,273 [400.8]		183 [58.3]
Off East Sakhalin					119 [19.0]	8 [0.9]	328 [35.0]		336 [35.9]	2 [1.4]	
Central Deep-Sea	2 [0.4]	79 [13.4]	831 [140.0]	912 [153.8]	29 [6.8]	1 [0.2]	41 [10.0]	28 [6.6]	70 [16.8]		
Southern Deep-Sea	0 [0]	0 [0]	701 [88.8]	701 [88.8]	2,567 [416.6]	14 [2.0]	28 [4.0]	0 [0]	42 [6.0]		
Off Kuril Chain	35 [3.4]	539 [52.8]	439 [43.1]	1,013 [99.3]	141 [18.1]	1 [0.1]	93 [11.0]	0 [0]	94 [11.1]		
Total Biomass	[16.9]	[368.7]	[273.1]	[658.7]	[1,627.0]	[36.2]	[427.0]	[7.4]	[463.2]	[1.4]	[58.3]

mesopelagic zone close to the bottom, where the biomass peaked at 1,627 thousand tons in august 1989. The data at hand also show that the mesopelagic zone usually accounts for up to 90-95% of the total squid biomass in the water column.

In the Pacific Ocean off the Kuril Islands, stock abundance assessments for *B. magister* were made using the so-called “trawl tracks” approach and were based on data collected by commercial bottom trawlers (Railko, 2005). Biomass assessments, based on catch statistics for this squid species off the central and north Kuril Islands, oscillated from 78 to 280 thousand tons during 1987-2011 (Figure 19).

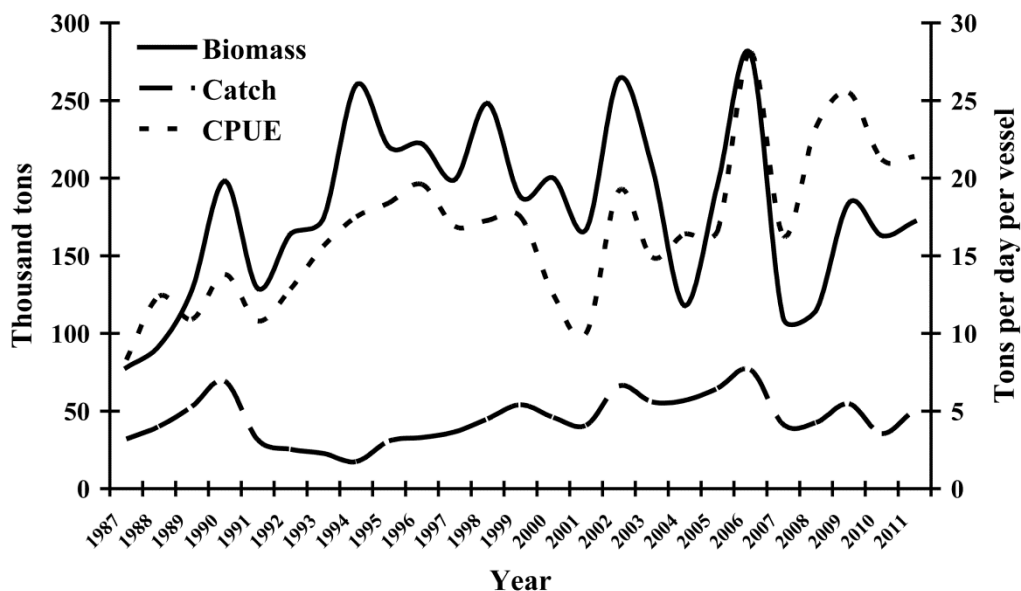


Figure 19. Estimated biomass (thousand tons), annual catch (thousand tons) and catch per unit effort (CPUE, tons per day per vessel) for *Berryteuthis magister* commercially harvested on the slope in the Pacific Ocean off the Kuril Islands.

It is worth noting that, due to rough bottom topography, paths for relatively safe bottom trawling in the region are located within a narrow depth range on the slope, generally in-between 270 and 450 m, which automatically leads to certain underestimation of the real squid biomass. The total area occupied by paths where bottom trawling is possible account for only 7-10% of the island slope area, where the squid occur in large quantities. Therefore, we may assume that the real stock biomass during peaks of the squid abundance is in fact much higher than the estimated figure. Bottom haul based stock assessments for *B. magister* in the northwestern Bering Sea, where the slope relief is rather even across vast areas, e.g., in-between capes Olutorskyi and Navarin, or in the Olutorskyi Bay, can be considered more reliable. However, even under these “favorable” conditions for direct stock assessments based on bottom trawling, biomass estimates may differ significantly. For example, instantaneous stock biomass was 6-13 times higher in autumn than in spring, and peaked at about 63 thousand tons, judging from bottom trawl surveys conducted during 1993-1995 on the slope in the Olutorskyi-Navarin region within depth range 200-700 m (Bizikov, 1996).

Biomass assessments, made for *B. magister* in autumn 1998 within practically the same area, yielded a much higher value, of about 190 thousand tons (Lapko et al., 1999). Such a discrepancy in estimates can hardly be attributable to natural stock variability, and most likely is associated with differences in stock assessments methods. Changes in stock abundance are reflected by variability in catches for the squid. In the western Bering Sea, major fishery areas for *B. magister* are located in the Olutorskiy Bay and along the Koryak coast (Olutorsko-Navarinskiy region), where total annual catch ranged from 0.55-9.02 thousand tons in the 1980s – early 1990s, and dropped down to 0.12-0.9 thousand tons during 1996-2003. Judging from trends in catches, the squid stocks living in the western Bering Sea and off the southeastern Kamchatka oscillate roughly in the out-of-phase manner. For example, CPUE for the squid estimated as catch per day per vessel declined from 30 tons in 2006 to 13 tons in 2009 in the western Bering Sea, and concurrently increased from 22.8 to 48 tons in the Pacific Ocean off Kamchatka.

4.4. Recruitment and Environmental Variability

Changes in *B. magister* catch and biomass in different are usually rather hard to interpret and, so far, no clear associations have been found between the squid catches (or stock abundance) and physical factors such as climate and oceanography. Relatively small but significant correlations were found between the squid CPUEs obtained during squid fishery off the central and north Kuril Islands on one hand, and regional pressure gradient on the other (Didenko et al., 2011). Local pressure gradient expressed as the difference between atmospheric pressure on the Iturup Island (Yuzhno-Kurilsk town) and southeastern Kamchatka (Petropavlovsk-Kamchatskiy city) is an indicator of monsoon strength in the southern Okhotsk Sea and adjacent areas: the greater the difference in pressure over the area, the stronger the northwesterly winds, and the weaker the inflow of Kuril-Kamchatka Current into the fishery area and the lesser the inflow of Pacific water into the Okhotsk Sea through the northern Kuril passes.

Changes in the local pressure gradient in turn serve as an indicator of changes in regional atmospheric circulation and reflect the position and structure of the Aleutian Low. It appeared that generally the greater was the pressure difference in the area, the lower were the squid catches off the Kuril Islands, and that pattern persisted across the seasons, being more evident during winter and spring months (Table 5).

Under such a scenario, an impact of changes in hydrology due to atmospheric pressure was expected to be stronger in the central Kuril region than in the north of the archipelago, which was indeed supported by higher negative correlation between catches and pressure difference anomalies in the centre ($R=-0.20$) than in the north ($R=-0.11$) of the Kuril Archipelago (Figure 20). On the decadal scale (1997-2010), squid catches were higher in 1997-2000 and 2006-2010, and lower in 2001-2005. Low catches were associated mainly with cold years, when Aleutian Low was shifted eastward of its long-term average position (with strong pressure gradient), and higher catches were mainly in warm years, when the Aleutian Low was located to the west of its “normal” position (with weak pressure gradient). These observations suggest that, in years, when due to the position of the Aleutian Low the winter monsoon was weak conditions for higher recruitment were more favorable.

Catch and biomass data were further used to construct a model, which will satisfactorily describe the observed annual fluctuations in commercial aggregations of *B. magister*, harvested off the Kuril Islands, with the aim to use such a model for predicting stock abundance of this species.

Continuous catch statistics for *B. magister* off the Kuril Islands (catch data are available from 1979 and biomass assessments from 1987) allows to use surplus production models for the analysis of stock variability (Babayan, 2000). The existing data were better described using surplus production model (Schaefer, 1954, 1957) in its modified version (Prager, 1994; Prager et al., 1996).

To improve the model, difference between the observed and model-predicted data were further compared with various North Pacific climate indices using maximum information criterion (MIC) (Reshef et al., 2011; Speed, 2011). Initially, the following climate indices were tested: AOIa, NPIa, PDOw, PDOs, PDOa, SAI, SI, AI, WPw, WPsp.

Table 5. Relationships (regression line slope and correlation coefficients, CC) between *Berryteuthis magister* catches off the central and northern Kuril Islands and pressure difference anomalies, and between catches in these two regions

	Slope (Catch/Pressure)			CC (Catch/Pressure)			CC (Catch/Catch)
	Central Kurils	North Kurils	Mean	Central Kurils	North Kurils	Mean	Central Kurils-North Kurils
Spring	-3.37	-1.20	-2.28	-0.39	-0.14	-0.31	0.43
Summer	-2.33	-3.13	-2.73	-0.19	-0.30	-0.30	0.33
Autumn	-0.62	-0.70	-0.66	-0.10	-0.11	-0.14	0.27
Winter	-1.88	-	-	-0.41	-	-	-
Year	-1.56	-0.95	-1.25	-0.22	-0.11	-0.19	0.40

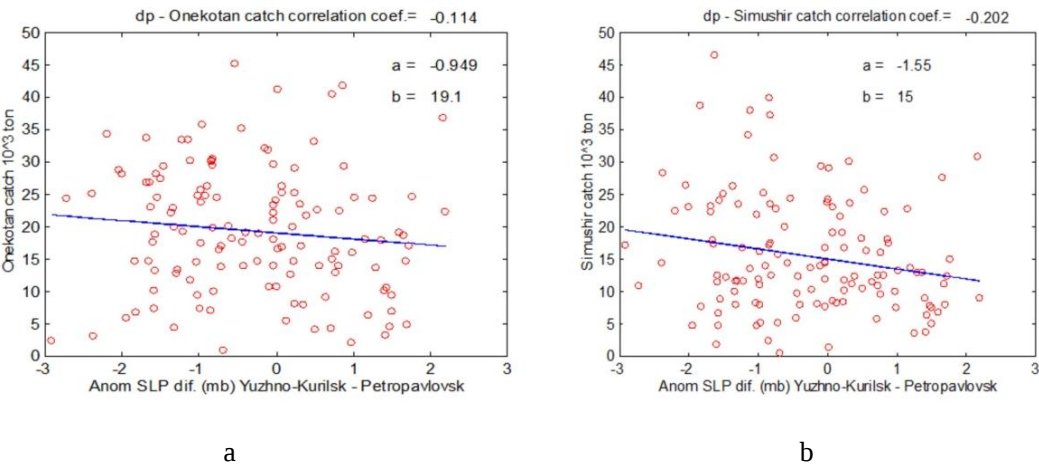


Figure 20. Correlation between anomalies in pressure difference along the Kuril Islands and *Berryteuthis magister* catches off the north (a) and central (b) Kuril Islands.

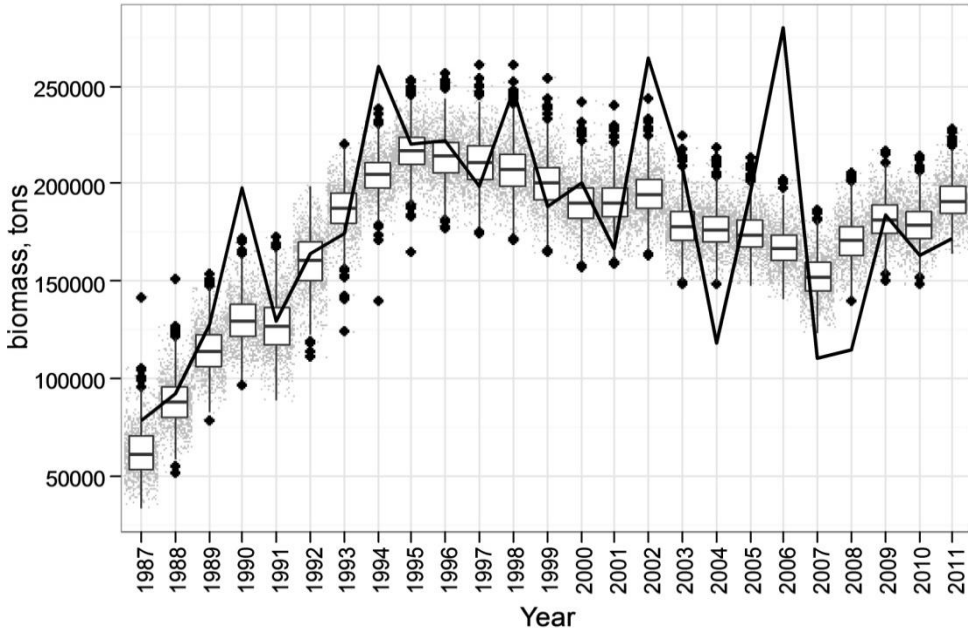


Figure 21. Estimated biomass (black solid line) and production model biomass values (box-and-whisker plots) for *Beryteuthis magister* harvested off the Kuril Islands.

Of these, only the Aleutian Low index (NPIa) (Kalnay et al., 1996) appeared to be correlated (negatively) with stock abundance of the squid in the Pacific Ocean off the Kuril Islands. Biomass values produced by the model (after 1,000 bootstrap iterations) appeared very close to biomass estimates, based on catch data (Figure 21). However, correlation between biomass residuals (differences between the observed and model values) and climate indices appeared rather weak, suggesting that climate indices do not improve the model significantly. Time series analysis showed significant (Kwiatkowski et al., 1992) one-year shifted autocorrelation. Thus we included shifted time series in further analysis.

In linear models, significant correlation was observed between annual squid catches in successive years. Of all climate indices tested in linear regression models only NPIa was able to improve the model: catches in successive years and NPIa accounted for about 90% and 10% of the model determination coefficient, respectively. We, therefore, tried to incorporate data from this climate index into the surplus production model in order to improve the ability of the model to describe the observed catch oscillations.

Though linear equations satisfactorily described the situation, relationships between catches in successive years better fitted logistic equation than linear or exponential. The resultant logistic curve is described by *formula 1*:

$$Y_{t+1} = \frac{a \cdot Y_t}{1 + b \cdot Y_t}, \text{ where } Y - \text{catch, } t - \text{year, } a \approx 1.89, b \approx 2.17 \cdot 10^{-5}.$$

Standardized residuals for catches, calculated using *formula 1*, negatively correlated with NPIa, which made it possible to include a coefficient for this climate index, and suggest a modified *formula 2*:

$$Y_{t+1} = \frac{a \cdot Y_t}{1 + b \cdot Y_t} + c \cdot I_t$$

where Y – catch, t – year, $a \approx 1.77$, $b \approx 1.67 \cdot 10^{-5}$, $c \approx -5576$, I – NPIa values.

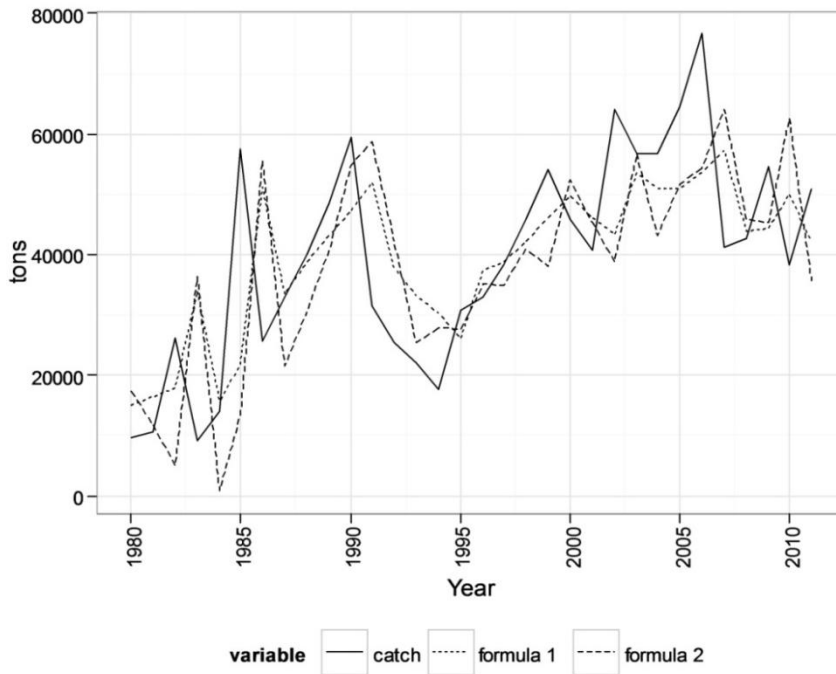


Figure 22. *Berryteuthis magister* actual catch (solid line) and predicted catch values (dashed lines), obtained from two equations: formula 1 (without NPIa coefficient) and formula 2 (with NPIa coefficient).

Information criterion (Akaike, 1974) for the second equation is less than for the first equation, thus suggesting that *formula 2* better describes changes in the squid catches than *formula 1*. Application of jack-knife procedure (Seber, Wild, 1989), which revealed strong influence of some annual catches on coefficients, improved the coefficients. Those were further used to produce graphs showing catch data, predicted by both models (Figure 22).

Undoubtedly, further studies are needed to fine-tune the model and improve its predictability for *B. magister*. So far, our data suggest that climate oscillations play relatively minor role, and other factors influencing recruitment (most likely, biological) underlie the observed patterns of stock fluctuations in this demersal squid species.

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Chapter II

***Illex coindetii*, Broadtail Shortfin Squid**

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Abstract

This paper constitutes an updated review of the biology, ecology and fisheries of the ommastrephid short-finned squid *Illex coindetii*, an oceanic and neritic species widely distributed in Atlantic and Mediterranean waters. *I. coindetii* seem to produce large numbers of small eggs. Their rhyncoteuthion paralarvae are small, less than 2 mm total length. Females are larger than males. Although this species spawns all year round, several ageing studies using statoliths detected two main growth groups in both sexes. Animals hatching in spring-summer grow faster than those hatched in autumn-winter. Its potential fecundity ranges from 3,500 to 300,000 oocytes. Spermatophore bunches are attached at the base of the female gills. This species is considered an intermittent terminal spawner and it does not seem to undertake large-scale migrations during its life cycle. It is a voracious predator, whose diet is composed of fish, crustaceans and cephalopods. Adults occur in the stomachs of various cetaceans, bony fishes, sharks, other squid and cannibalism has also been detected. Helminth infection studies revealed a homogeneous group of orally acquired endoparasites. The high prevalence infestation by *Pennella* implied the reduction in condition of these squids. Even though it seems that *I. coindetii* from the Atlantic and the Mediterranean Sea is a single variable species, further studies are needed to understand the causes of the existence of a high number of more or less distinct morphotypes. *Illex coindetii* play an essential role in the oceanic system acting as an ‘ecosystem accelerator’, since these are animals with high food intake and high conversion rates thus increasing rates of energy transformation and accumulating high quality protein, available to higher consumers. The species has an important commercial value in many areas of the European waters. The life cycle of this species is coupled to atmospheric-oceanographic parameters. There is no analytical assessment or fishery forecasting carried out for *Illex coindetii*.

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1. Introduction

It's been a long time since Young (1934) discovered the epistellar body in the stellate ganglion of cephalopod giant axons. These studies allowed him to lead the pioneering research that ended in the present wide knowledge of the cephalopod nervous system. This system allows these marine molluscs, among other skills, to respond rapidly to external stimulus, change direction rapidly, undertake defence movements and perform easy displacements. A clear example of effectiveness in displacement behaviour is found in some ommastrephid species, such as *Illex coindetii* Vérany, 1830, which is able to jump outside the water up to 6 m height and distances of over 50 m long (Akimushkin, 1963). The common name of this species is related to the above and thus is named "flying squid" in some areas of its distribution range.

The family Ommastrephidae Steenstrup, 1857, which includes *Illex coindetii*, is composed by oceanic and neritic species. This is one of the most widely distributed and conspicuous families of squids in the world. Ommastrephids are powerful swimmers and some species form large schools (Roper et al., 2010).

One of the common characteristics of the genus *Illex* is related with their geographic distribution, since all of them are mostly restricted to the Atlantic waters. The main problem found is the overlapping of the areas occupied by three of the four *Illex* species because *Illex argentinus* has a very distinct and restricted geographical distribution. It is difficult to differentiate between *I. coindetii*, *I. illecebrosus* and *I. oxygonius* in areas where they are overlapped based on morphological characters. In fact, for many years, some experts doubted that *I. oxygonius* were a valid species. However, Roper et al. (1998) undertook a detailed study on the matter and concluded that four species were valid. Martínez et al. (2005a) using allozyme polymorphisms confirmed the valid specific status of the four species above mentioned.

The main taxonomical characteristics of *I. coindetii* are the presence of two rows of suckers in the arms, an inverted t-shaped funnel cartilage and eight rows of suckers on the tentacular dactylus. Fins are terminal and their length is always less than 50% of the mantle length (Guerra, 1992). This species possesses a fin wide, and a fin width to length ratio 1,4-1,5, with a fin angle (angle formed by posterior edges of fins) of more than 50°. Either right or left ventral arms are hectocotylized and the hectocotylus is complex (Guerra, 1992; Roper et al., 2010); its development has been recently studied by Zecchini et al. (2012). A detailed analysis of morphological variability of *I. coindetii* along the North West coast of Africa is reported in Hernández-García and Castro (1998).

Although the species was firstly revised 13 years ago (Sánchez et al., 1998), since then several studies were undertaken, which increased the existing information for the species throughout its distributional range. Even though little information on the ecology of *Illex coindetii* is available at present, based on evidences recorded for the congener species, it seems that it would make good use of environmental conditions that provide appropriate combinations of: 1) trophic enrichment 2) concentration processes 3) currents/transportation regimes (Bakun and Csirke, 1998). Recently, the effect of frontal zones movement and peculiar hydrographic conditions (due to changes in the general hydrological pattern) on *I. coindetii* distribution and abundance in the Sicilian Channel was in fact evidenced (Jereb et al., 2001).

The bibliography available for this species, in comparison with the other two congeners of commercial importance, *Illex argentinus* e *Illex illecebrosus*, is relatively scarce. Here we compiled an updated review of the biology, fishery characteristics and ecological aspects along the whole distribution range of *Illex coindetii*, considered as a short life-span renewable resource. We will show the present perspective of the reproduction, ageing, trophic ecology, fisheries and also potential influence of oceanography on the sustainability of this species, as a resource, in the future.

2. Life History Biology

2.1. Early Stages

Similarly to their conspecifics, *Illex coindetii* seem to produce large numbers of small eggs, ranging from 0.8 to 1.3 mm (Boletzky et al., 1973; González et al., 1994a; González et al., 1996a; Hernández-García, 2002), encapsulated in gelatinous masses that either float on or near the surface or settle on the bottom.

The only record of egg masses of the *Illex* species found in nature was cited by Naef (1928), who described a large floating mass in the Mediterranean Sea, near Naples. However, visual observations and video-tape records of the spawning of the congener captive *Illex illecebrosus* from the northwest Atlantic (e.g., Durward et al., 1980; Balch et al., 1985; O'Dor and Balch, 1985), showed that this species can produce spherical, semitransparent, gelatinous and floating egg masses while swimming in open water. While these observations do not rule out spawning on the bottom, they made it clear that *Illex* species can spawn in the pelagic domain.

Laboratory observations, in conditions of artificially aerated sea water (Boletzky et al., 1973), indicate that the egg jelly is completely transparent and that the egg chorion strongly swells during embryonic development, attaining a diameter of about 2 mm at the moment of hatching, to accommodate for the paralarvae total length (ML) of 1.4 mm. As reported by Boletzky et al. (1973), the embryonic development would follow the description given by Naef (1928) for a number of ommastrephids, and its success depends on water temperature. At 10°C the eggs did not develop and degenerate; at 15°C the development was “normal”, while at 20-22°C it was much faster and many paralarvae hatched prematurely. This evidence suggests that embryonic development will take about 10-14 days at 15°C and that optimal temperature must not be much lower, as reported also for *I. illecebrosus*, for which temperatures above 13°C are necessary for a successful embryonic development (O'Dor et al., 1982).

Similarly to other ommastrephid paralarvae (rynhoteuthion), *I. coindetii* early stages of development are small, less than 2 mm in total length (e.g. O'Dor et al., 1985). They hatch only with the two dorsal pairs of arms and a proboscis, which later divides to form the tentacles of the adults. Hatching of the rynchoteuthion paralarvae occurs after a few days to a few weeks. Post spawning mortality is high. Some of these observations were reinforced by Villanueva et al. (2011), who developed in vitro fertilization techniques of *I. coindetii* from the Mediterranean Sea. They observed that egg and hatchling sizes of these ommastrephids are close to the minimum for cephalopod species (Figure 1).

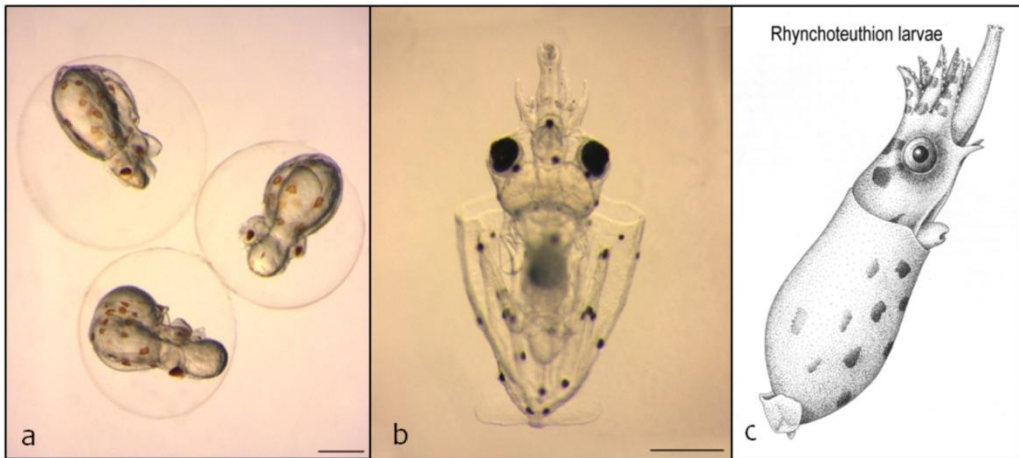


Figure 1. Different rhynchoteuthion stages of *Illex coindetii*. a) Embryos aged 164 h and photographed 25 h after receiving the third oviducal gland jelly addition (Villanueva et al., 2011); b) A dorsal view of an individual aged 427 h after fertilization (e.g., 8 d after reaching the hatchling stage 30) and incubated at 17 °C (Villanueva et al., 2011); c) Rhynchoteuthion after Guerra (1992). Scale bars = 0.5 mm.

Low incubation densities and the use of antibiotics resulted in relatively high survival rates to hatchling. Hatching time was inversely proportional to incubation temperature and ranged from 5 to 11 days at 21 °C and 13 °C, respectively. They also noted that larger hatchlings in length and weight also tended to be produced at low temperature, probably also due to better yolk absorption.

Morphologically, the youngest forms of *Illex coindetii*, *I. argentinus*, *I. illecebrosus* and *I. oxygonius* cannot be clearly distinguished (Sweeney et al. 1992). Common features at this paralarval stage are: no ocular or visceral photophores; suckers on proboscis tip nearly equal in size; proboscis length typically 50-75% ML; proboscis division begins at 4.0 mm ML and is completed at 10 mm ML. This uncertainty should encourage performing molecular studies and in vitro fertilization studies targeting the correct identification of these complex and understudied ommastrephid paralarvae.

In the wild, rhynchoteuthion paralarvae, some of them potentially *I. coindetii*, were collected off the Atlantic and Mediterranean coasts (Sánchez and Moli, 1985; Moreno et al., 2009; González, unpublished data). Rhynchoteuthion ranging from 1.3 to 3.7 mm ML, classified by us as type A, which are remarkably similar to those fertilized in vitro by Villanueva et al. (2011), showed the following main characteristics: 1) pair of arms I and II present but short, pair III large and pair IV very short; 2) Proboscis 38-41% ML; however we have to take this with caution because this is a retractile organ; 3) Eight suckers in the tip of the proboscis, of similar size except the central ones that are slightly larger than the others; 4) the relation between maximum mantle width and the maximum fin width ranged between 30-35%; 5) Ocular or visceral photophores absent.

In northwestern Spanish (Galicia) and Portuguese waters, rhynchoteuthion were collected all year round on the shelf and shelf break between the 30 and 300 m isobaths. Generalised linear models highlight the higher probability of capture of ommastrephid paralarvae at northern latitudes in Portuguese waters. The interaction latitude versus month was also significant, reflecting the seasonal variation in the spatial distribution: during spring/summer most paralarvae occurred on the northern shelf and meridional spread from the centre of

distribution was detected in autumn/winter. During winter, some specimens occurred in oceanic waters, namely between the continental shelf-break and oceanic seamounts (Galicia and Gorringe Banks). The distribution of paralarvae was limited to SST between 13 and 20°C (Moreno et al., 2009).

2.2. Growth and Age

In *Illex coindetii*, a medium size squid, females are larger than males throughout the distribution range (Figure 2).

The maximum mantle length, however, depends on the population examined. Thus, the larger animals ever found were 370 and 320 mm ML for females and males, respectively. These animals were collected in northern Galician waters (González et al., 1996b). Size values for animals distributed in the Spanish Mediterranean are 170 mm for females and 140 mm for males (Sánchez, 1984), while in the French waters in the Mediterranean are 263 mm and 200 mm respectively for females and males (Mangold-Wirz, 1963). In the northern Tyrrhenian Sea maximum ML for females is 245 mm and 175 for males (Belcari et al., 1989), while information from the central Tyrrhenian (Gentiloni et al., 2001) indicates lower maximum sizes (200 mm) for the population examined. In the Central Mediterranean and in particular the Sicilian Channel largest females measured 230 mm and largest males 180 mm (Jereb and Ragonese, 1995) while in the Adriatic Sea values reported are 280 and 183 mm for females and males respectively (Soro and Paolini, 1994).



Figure 2. Ventral and dorsal view of an *Illex coindetii* specimen collected in Galician waters (195 mm ML).

Table 1. Summary of studies performed to date dealing with age and growth rate estimations in all areas inhabited by *I. coindetii*

	Growth rate (mm day ⁻¹)		Life span (m)		Area	Reference
	Females	Males	Female	Male		
DA	0.84	0.72	15	13	Northeastern Atlantic (NW Spain)	González et al., 1996
DA	1.6	1.4	8	6	Central-eastern Atlantic (Sierra Leone)	Arkhipkin, 1996
DA	1.4	0.8	10	8	Central-eastern Atlantic (Western Sahara)	Arkhipkin, 1996
DA	1.11	-	12	12	Eastern Atlantic	Sánchez et al., 1998
DA	0.44	-	16	16	Western Mediterranean	Sánchez et al., 1998
DA	1.4-1.78	1.15-1.55	6-7	6-7	Central Mediterranean (South Italy)	Arkhipkin, 2000
MPA	0.39-0.43	0.33-0.34	24	12-20	Western Mediterranean	Manglod-Wirz, 1963
MPA	0.47	0.38	18	17	Western Mediterranean	Sánchez, 1984
MPA	0.30-0.83	0.50-0.86	15	15	Northeastern Atlantic	González, 1994
MPA	0.32-0.45	0.32-0.45	14-16	14-16	Central Mediterranean	Jereb and Ragonese, 1995
MPA	0.67	0.73	18	11	Northeastern Atlantic	Arvanitidis et al., 2002
MPA	0.92	-	13	-	Northeastern Atlantic	Arvanitidis et al., 2002
MPA	0.82	0.84	15	10	Eastern Mediterranean	Arvanitidis et al., 2002

MPA: Modal Progression Analysis; DA: Direct ageing.

In the eastern part of the Mediterranean (Greek waters) maximum recorded ML values for females usually are up to 220 mm and up to 200 mm for males, even though extreme values have been reported (a female of 352 mm— Arvanitidis et al., 2002). Smaller values have been recorded from the Levantine basin (180 and 145 mm for females and males respectively - Cyprus waters - Salman et al., 1998) and from the Sea of Marmara (140 mm for females and 165 mm for males - Katagan et al., 1993).

This species shows sexual differences in the length-weight relationship (Ragonese and Jereb, 1990; Belcari, 1996; González et al., 1996a; Sánchez et al., 1998, Arvanitidis et al., 2002; Ragonese et al., 2002). ML instantaneous relative growth rate differs between areas. Absolute growth rates varied from 0.44 to 1.78 mm day⁻¹ for females and from 0.8 to 1.55 mm day⁻¹ in males. Growth rates in both sexes were dependent of the season of hatching. Squids hatched in winter attained larger sizes for the same age than squids hatched in other seasons. These seasonal differences in growth were only evident after squids reached eight months of age.

Comparison of the relationship between ML (mm) and total weight (TW, g) in different regions of the Mediterranean and the Eastern Atlantic indicates a positive allometric growth for males, while isometric growth and allometric growth, both positive or negative, have been reported for females (Table 1). In the latter case, the values of the coefficient b are always significantly lower than in males (Ragonese and Jereb, 1992; Belcari, 1996; Sánchez et al., 1998; González et al., 1996b; Arvanitidis et al., 2002). This result accounts for the morphometric sexual dimorphism demonstrated in adult animals and is shown especially when size increases and males exhibit a strongly marked increase in head width and in the brachial apparatus. The maturation process affects the length-weight relationship, immature individuals generally revealing negative allometric growth independently on sex; the typical trend for each sex starts with the maturation process (Belcari, 1996). However, González et al. (1996b) in the northeastern Atlantic found that immature and mature males showed a positive allometry whilst immature and mature females showed negative allometry.

Two of the most widely used methods for estimating age in cephalopods are Modal Progression Analysis (MPA) and analysis of size-at-age data, based on growth increments in statoliths. In many cephalopod species, such as *I. coindetii*, due to its extended spawning season and possible migration, MPA is unable to discriminate clearly among different microcohorts in a population, as Caddy (1991) postulated from a theoretical point of view.

Although *I. coindetii* spawns all year round, which provokes the potential appearance of several microcohorts in a single year (González, 1994; Arvanitidis et al., 2002), several studies on age determination using the growth increments in the statoliths detected two main growth groups in both sexes, depending on the hatching period. Animals hatched in spring-summer show slightly faster growth than those hatched in autumn-winter (Sánchez, 1995; González et al., 1996a; Arkhipkin et al., 2000).

Examination of statoliths has been shown to be the most reliable method to age *Illex* species (González et al., 2000). The first satisfactory attempts to determine age from statoliths were performed by Lipinski (1978) on the short-finned squid *Illex illecebrosus*. This author found periodic growth increments, which they considered to occur daily. There were others more broadly spaced that they considered to occur monthly. Since this first approximation, age of various cephalopod species has been studied based on growth increments in statoliths (González and Guerra, 1996; Arkhipkin et al., 1998). In several species kept in captivity, whose statoliths were marked with strontium (Hurley et al., 1985) or with tetracycline (Dawe et al., 1985; Jackson, 1990), the hypothesis that increment deposition is daily has thus been validated. According to estimations made using these methods, its life span is about one year for males and females. The age at which individuals mature is variable, ranging from 100 to 271 days in males and from 140 and 285 in females (Pierce et al., 2010).

2.3. Maturation, Fecundity and Sex Ratio

Illex coindetii spawns throughout the year, with seasonal peaks varying widely (frequently with one or two peaks of maturation, the spring-summer being the most evident) through the geographical range (Pierce et al., 2010). Potential fecundity ranges from 3,500 to 300,000 oocytes (the most frequent range being from 30,000 to 200,000 oocytes). Eggs are small ranging from 0.8 to 1.3 mm (major axis), and they are possibly laid in jelly masses near the bottom on the continental slope at mid waters, free from any attachment.

Copulated females of *I. coindetii* allocate for fertilization one or several spermatophore bunches attached by males to the base of their gills. These bunches contain a minimum of 20 to a maximum of 1555 (Nigmatullin and Vovk, 1972; González and Guerra, 1996). This species can be considered an intermittent terminal spawner (Rocha et al., 2001). Four signs support the hypothesis of the existence of intermittent spawning in *I. coindetii*: a) The existence of spermatophore bunches with different morphology in certain mature females and their relationship with the spawn; b) Only weak relationships between fecundity and t ML, and between number of eggs in the oviduct and ML were found. It is worth noting that if the females increase in size once maturity is attained and there is an important variation in the fecundity of females of the same size, this seems to suggest that these females spawn intermittently. Harman et al. (1989) indicated similar results for *Sthenoteuthis oualaniensis* to those observed for *I. coindetii*; c) The ovaric index in mature females, and d) Observations of pre-vitellogenic and vitellogenic oocytes in the ovary (see González and Guerra, 1996).

Based on the nidamental gland index ($NGI = NGL \times ML^{-1} \times 100$), it was possible to differentiate between the stages of sexual maturity in female *I. coindetii* (González and Guerra, 1996). Nidamental gland length allows distinguishing roughly between three physiological conditions (immature, preparatory and mature) using a quantitative data, which increases the accuracy in relation to the assessment with subjective criteria. Although this parameter in isolation cannot be used to differentiate maturity stages, it is interesting from the perspective of fishery science or whenever large and quick samplings should be done.

Mature specimens are found in a wide size range. Across its geographic distribution, *I. coindetii* males mature at a lesser mantle length and attain a smaller size than females (see Table 2). Size at maturity ($ML_{50\%}$ values) indicates some degree of geographic variation in both sexes, showing a north-south gradient in *I. coindetii* populations from the Northwest towards the Central-eastern Atlantic, as well as a west-east gradient of decreasing values, from the North Atlantic to the Eastern Mediterranean (CEPHSTOCK, 2005). Thus, higher $ML_{50\%}$ values have been reported for populations from the most distal areas in the Central and Eastern Atlantic (i.e. Southern Celtic Sea and Bay of Biscay and North-western Africa); intermediate values from the Atlantic areas proximal to the Mediterranean (i.e. Galician waters and Portuguese waters) and lower values from the Mediterranean (i.e. straits of Sicily and Greek Seas). Mature as well as maturing specimens are found within each depth range throughout the year, even though in different proportion according to months (e.g., Jereb and Ragonese, 1995). The existence of one (Southern Celtic Sea-Bay of Biscay and Galician waters) or, potentially, two (Portuguese waters and, more clearly, in Greek Seas) mode sizes at maturity may suggest two reproductive strategies of the species along the Atlantic and the Mediterranean (Arvanitidis et al., 2002).

Sex ratio was close to 1:1 in most studies dealing with *I. coindetii* populations in the Western Africa and Catalanian Sea (Sánchez et al., 1998), Sicilian Channel (Jereb and Ragonese, 1995), Adriatic Sea (Petric et al., 2010), Southern Celtic Sea and Bay of Biscay, Portuguese waters and Greek Seas (Arvanitidis et al., 2002) and slight deviations from this ratio have been mostly attributed to occasional variations in population structure (Sánchez et al., 1998). However, significant deviations in sex ratio have been recorded in *I. coindetii* populations from the Galician waters (González and Guerra, 1996) and also from the Ionian Sea (Tursi and D'Onghia, 1992).

It seems that the energy used for the egg production is taken directly from food rather than from stored products in *Illex coindetii* as well as *Todaropsis eblanae*. On the other hand,

a significant increase in the content of lipid and fatty acids was observed in the gonad and digestive gland of both species during sexual maturation. However, there was no evidence that storage reserves are transferred from tissue to tissue (Rosa et al., 2005).

Table 2. Comparison of size at maturity (ML_{50%} values) of *Illex coindetii* populations from the Mediterranean and the Central and North Eastern Atlantic

Area		Female	Male	Reference	
Northeastern Atlantic (S Celtic Sea- Bay of Biscay)		248	153	Arvanitidis <i>et al.</i> , 2002	
Northeastern Atlantic (Galicia, NW Spain)		184	128	González and Guerra, 1996	
Northeastern Atlantic (Portuguese waters)		181	129	Arvanitidis <i>et al.</i> , 2002	
Central-eastern Atlantic (Morocco and Sahara)		218	166	Hernández-García, 2002	
Central-eastern Atlantic (NW Africa)		208	160	Hernández-García and Castro, 1995	
Central-eastern Atlantic (Mauritania to Sierra Leone)		190	153	Hernández-García, 2002	
Central-eastern Atlantic (Sierra Leone to Liberia)		167	127	Hernández-García, 2002	
Central Mediterranean (Sicilian Channel)		150	120	Jereb and Ragonese, 1995	
Central Mediterranean (SW Adriatic Sea)		146	137	Ceriola <i>et al.</i> , 2006	
Eastern Mediterranean (Greek Seas)		179	113	Arvanitidis <i>et al.</i> , 2002	

3. Ecology

3.1. Distribution and Abundance

The geographic distribution of *Illex coindetii* is disjunct. It extends throughout the Mediterranean Sea, East Atlantic from the British Isles and the Oslo Fjord (60°N) to Namibia (20°S) and West Atlantic in the proximities of the Gulf of Mexico and the Caribbean Sea, from Virginia coast (37°N) to French Guiana waters (approximately 3°N) (Nesis, 1987; Guerra, 1992; Roper et al., 2010). This species was also cited in the Red Sea (Adam, 1942), but this is likely to be a mislabelled cite (Lu, 1973). *I. coindetii* occurs from the surface to over 1100 m, with maximal concentration between 100 and 400/600 m, depending on the area considered (e.g., Sánchez *et al.*, 1998). It lives close to muddy, sandy, and detritic bottoms, often covered by *Funiculina* spp. (Mangold-Wirz, 1963; Roper et al., 2010).

3.2. Migrations

Illex coindetii live at the bottom in the middle and lower sub-littoral and upper bathyal, in temperate latitudes. They undertake vertical migrations from the bottom (day) to the surface (daytime). Abundance indices for 21 cruises of fish prospection performed on the continental slope and shelf off the north-western Spain (30-500 m depth) between 1973 and 1991 showed that *Illex coindetii* appeared in this zone, in significant numbers in 1984 and peaking in 1987.

In spite of what seems to occur with their congeneric *Illex illecebosus* (Dawe *et al.*, 1981) and *Illex argentinus*, *Illex coindetii* do not undertake large-scale migrations during their life cycle. At least, this is what may be inferred from the data gathered in the Atlantic and Mediterranean waters, where animals of all maturity stages were found throughout the year in the same area (González and Guerra, 1996; Arvanitidis *et al.*, 2002).

3.3. Trophic Ecology

3.3.1. *Illex Coindetii* as Predator

Illex coindetii is a voracious predator, which diet is composed by, in decreasing order of importance, fish, crustaceans and cephalopods (Table 3).

It was also noted the presence of cannibalism. Crustaceans are relatively more important as prey in smaller squid (Figure 3). As the squid grow, fish and cephalopods become increasingly important prey (Lordan *et al.*, 1998). *I. coindetii* is mainly a neritic nekto-benthic predator with wide spectra of prey. It has been found associated with decapod crustaceans, like *Parapenaeus longirostris*, and, more significantly, with fish like *Maurolicus muelleri*, *Merluccius merluccius* and *Micromesistius poutassou* (Sánchez, 1982; Rasero *et al.*, 1996, Dawe and Brodziak, 1998; Lordan *et al.*, 1998), often along with the lesser flying squid *Todaropsis eblanae* (e.g., Mangold-Wirz, 1963; Rasero *et al.*, 1996).

Table 3. Main preys of *Illex coindetii* (This table should be in the same page)

Group	Prey species
Fish	Myctophidae
	<i>Diaphus</i> sp.
	Sternoptychidae
	Pearlside <i>Maurolicus muelleri</i>
	Hatchetfish <i>Argyropelecus hemigymnus</i>
	Clupeiformes
	European anchovy <i>Engraulis encrasicolus</i>
	European pilchard <i>Sardina pilchardus</i>
	European sprat <i>Sprattus sprattus</i>
	Argentinidae
	Argentine <i>Argentina sphyraena</i>
	Gadidae
	Blue whiting <i>Micromesistius poutassou</i>
	Silvery pout <i>Gadiculus argenteus</i>
	Hake <i>Merluccius merluccius</i>
	Gobidae
	Transparent goby <i>Aphia minuta</i>
	Carangidae
	Horse mackerel <i>Trachurus trachurus</i>
	Scombridae
	Mackerel <i>Scomber scombrus</i>

Group	Prey species
Crustaceans	<i>Meganyctiphanes norvegica</i> <i>Sergestes robustus</i> <i>Dichelopandalus bonnieri</i> <i>Pasiphaea sivado</i> <i>Pasiphaea multidentata</i> <i>Parapenaeus longirostris</i> <i>Plesionika martia</i> <i>Polybius henslowii</i>
Molluscs	Cephalopoda <i>Alloteuthis</i> sp. <i>Illex coindetii</i> <i>Todaropsis eblanae</i> <i>Todarodes sagittatus</i> <i>Loligo forbesi</i> <i>Eledone cirrhosa</i> <i>Sepietta oweniana</i> <i>Rossia macrosoma</i> Gastropoda <i>Limacina inflata</i> <i>Limacina retroversa</i>

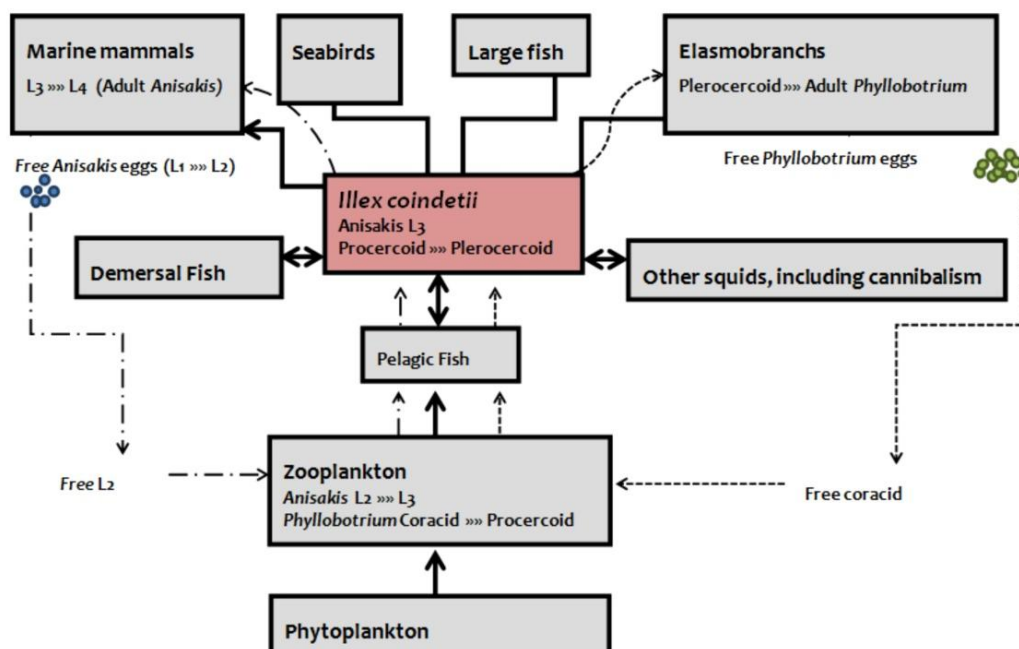


Figure 3. Proposed trophic web of *Illex coindetii* including its parasite relations.

3.3.2. *Illex Coindetii* as Prey

Table 4 summarizes the identified predators of *I. coindetii* throughout its distribution area. No information on predators of larval and small *Illex* juveniles is available at present (e.g. Dawe and Brodziak, 1998). Adults occur in the stomachs of various cetaceans, like *Grampus griseus*, *Tursiops truncatus* (Santos et al., 1997, 2007), *Globicephala melas*, *Delphinus delphis* (González et al., 1994b; Silva, 1999), bony fishes, like *Thunnus albacares* (Dragovich, 1970, in Smale, 1996), *Xiphias gladius* (Bello, 1985; Moreira, 1990), *Phycis blennoides* (Morte et al., 2002), *Conger conger* (Lordan et al., 1998) and sharks, like, for example, *Heptranchias perlo* (Henderson and Williams, 2001).

Data on the diet of Mediterranean commercial fishes are scant, but *I. coindetii* is one of the four cephalopods occurring in about 17-20% of large blue whiting stomachs in the Spanish Mediterranean (MacPherson, 1978; Sánchez, unpubl. data, in Dawe and Brodziak, 1998). Also, it is likely to be fed upon by other squid like, for example, *Todarodes sagittatus*, *Loligo vulgaris* of larger sizes and cannibalism has also been detected (Rasero et al., 1996; Dawe and Brodziak, 1998; CEPHSTOCK, 2005).

Table 4. Main predators of *Illex coindetii*

Predators		References
Marine mammals	<i>Grampus griseus</i>	Santos et al., 1997
	<i>Tursiops truncatus</i>	Gonzalez et al., 1994a ; Santos et al., 1997
	<i>Globicephala melas</i>	Gonzalez et al., 1994a
	<i>Delphinus delphis</i> <i>Kogia breviceps</i> <i>Pseudorca crassidens</i> <i>Physeter macrocephalus</i> <i>Ziphius cavirostris</i>	González et al., 1994a; Silva, 1999 Hastie et al., 2009 Hastie et al., 2009 Hastie et al., 2009 Hastie et al., 2009
Fish	<i>Heptranchias perlo</i>	Henderson and Williams, 2001
	<i>Xiphias gladius</i>	Bello, 1985; Moreira 1990
	<i>Thunnus albacores</i> <i>Centroscymnus coelolepis</i>	Dragovich, 1970 Hastie et al., 2009
	<i>Micromesistius poutassou</i>	Mac Pherson, 1978
	<i>Phycis blennoides</i>	Morte et al., 2002
	<i>Conger conger</i> <i>Pollachius virens</i>	Lordan et al., 1998 Lordan et al., 1998
Birds	<i>Calonectris diomedea</i>	Hastie et al., 2009
Cephalopods	<i>Loligo vulgaris</i> <i>Todarodes sagittatus</i>	Dawe and Brodziak, 1998 Dawe and Brodziak, 1998
	<i>Illex coindetii</i>	Rasero et al., 1996 ; Lordan et al., 1998
	<i>Todaropsis eblanae</i>	Rasero et al., 1996 ; Lordan et al., 1998

3.3.3. Parasites

Changes in the structure of ecosystems, whether artificial or natural, can influence ecological traits of different organisms, including parasite populations and communities (Sousa and Grosholz, 1991; Marcogliese, 2001). Environmental stress and exploitation may also cause shifts in the distribution and abundance of host populations, and in turn in their parasite communities (Gardner and Campbell, 1992; Marcogliese and Cone, 1997a, b). In general, unstable water masses seem to produce impoverished parasite faunas, especially for heteroxenous parasites with complex, multiple-host life cycles.

A rich anisakid fauna was found consistently in cephalopods from cold waters not influenced by an upwelling system (i.e. Grand Sole and Argentinean fishing grounds), but they were absent in samples from the Sahara Bank (a persistent upwelling area). Large-scale Russian surveys of the distribution of anisakid larvae in neritic squids from the west coasts of northern Africa (Gaevskaya and Nigmatullin, 1975) are consistent with this pattern; examination of 1880 mature *I. coindetii* revealed a low prevalence (P) of only 0.7% (meaning of prevalence $\frac{1}{4}$ infection rate of individual squid; i.e. 0.7% of all squid were infected).

Helminth infection studies in north-western Spanish waters (Galician waters) identified several genera of tetrathyllidean plerocercoids in *I. coindetii* specimens (prevalences: *Phyllobothrium* sp., 45.7%; *Dinobothrium* sp., 0.8%; and *Pelichnibothrium speciosum*, 0.001 %) and atrypanorhynchidean metacestode (*Nybelinia vamagutii*, 0.4 %). In addition, larval nematodes of *Anisakis simplex* (L3) were recorded (10.6%). These analyses revealed a homogeneous group of orally acquired endoparasites (Pascual et al., 1994, 1995). It is worthy of notice that all the cosmopolitan parasites (i.e. broad generalist species) *Phyllobothrium* sp., *Anisakis simplex* are 'component' species (*sensu* Bush et al., 1990) in this area (Figure 3). In this sense, we can assume that a typical 'ecological niche-widening' phenomenon (Mas Coma, 1991) is taking place here. The increase in host-dependent infection values suggest that the various size-maturity groups of squid apparently take part in different ways in the life cycle of *Phyllobothrium* sp., being the second and/or third intermediate hosts. However, at least in the case of long-lived digestive parasites, those differences may also simply be due to an accumulation of worms over time as a result of the predatory behaviour of squid (Naidenova et al., 1985).

The interannual values of prevalence of infestation of *Pennella* were 90% in *I. coindetii* and *Todaropsis eblanae*. This infestation implied that some 2.1% of the variation in condition of *I. coindetii* was reduced by about 8.8% (Pascual et al., 1998). If only the biomass of the exploited stock is considered for a 10 year period in the 90's or taking into account that landings during this period were about 13,000 tonnes (González et al., 1996c), and that 50% of the landings belong to each of the mentioned ommastrephid species, it can be inferred that the reduction in biomass of infested squid (considering only the exploited stock and do not its real) were 5,148 tonnes for *I. coindetii*. Assuming an average value of 0.8€/kg of squid, it can be inferred that the infestation of *Pennella* meant losses of about 1 million € for the period 1980-1991 (Pascual et al., 1998). A marked seasonal pattern in the number of this parasite copepod was observed in the northern area of Galician waters whereas these patterns were not detected in squids of the western area. These spatial and seasonal patterns in the parasite infestation could be attributed to biotic factors linked to host characteristics, i.e. onshore-offshore migrations but also to environmental variables (Pascual et al., 2001).

This overview highlights that parasitism is not only an important zoonotic problem but an important economic problem at the time of management of infested stocks, as previously reported by several authors in some other fisheries.

4. Fisheries

4.1. Stock Definition, Fishing Areas and Fishing Methods

Spanish and other European fleets harvest ommastrephid squid stocks from the northeastern Atlantic throughout the year (Hastie et al., 2009). They are usually taken as by-catch during demersal and pelagic trawling operations and in gill and trammel nets, in depths of 100–400 m (Mangold and Boletzky, 1987; Jereb and Ragonese, 1991; González et al., 1994; González et al., 1996c). Different species (predominantly *Illex coindetii* and *Todaropsis eblanae*) are often landed together as mixed ‘short-fin’ squid. Thus, landings data for individual ommastrephid species are often unavailable. Nevertheless, ommastrephid squid stocks are now regarded to be a high-value fishery resource (Jereb and Ragonese, 1995). During the past decade, the total ommastrephid catch in European waters has ranged from 3000 to 7000 t annually (Anonymous, 2004).

Even though comprehensive analyses seem to indicate that *I. coindetii* from the Atlantic and the Mediterranean Sea is a single, widely distributed, highly plastic and variable species (Roper and Mangold, 1998; Roper et al., 1998), also a general consensus exists on the need for further studies and investigations focused to understand the causes at the base of the existence of such a high number of these more or less distinct morphotypes. Specimens from different areas sometimes look strikingly different from the “typical” *Illex* from the Catalanian region (Roper and Mangold, 1998); these morphotypes are not well defined nor understood at present, and seem related not only to geographical distribution, but also to local and regional environmental factors.

In spite of this apparent high degree of variation in general *habitus* existing across the geographical range, the characters associated with the hectocotylus are surprisingly constant as, it seems, the indices of head and mantle width (see Roper and Mangold, 1998 for details).

Very large specimens, in excess of 250 mm ML are occasionally captured, on both sides of the Atlantic (i.e., Straits of Florida and Galician waters, in Roper and Mangold, 1998; González et al. 1996a) as well as in the Mediterranean (i.e., Greek waters, Arvanitidis et al., 2002). However, they seem to represent a small fraction of the population and co-occur with much more numerous, smaller, fully mature specimens.

As it seems the case with other ommastrephids (e.g., Cuccu et al., 2005), these unusually large specimens may represent late-hatching members of the previous year class, or at least individuals that for some reason do not reach maturity; consequently, they do not spawn and would appear to continue to grow, a phenomenon already suggested also for exceptionally large *Loligo pealei* in the western Atlantic more than one century ago (i.e., Verrill, 1881, in Roper and Mangold, 1998).

Genetic analyses of seven populations of *I. coindetii* from Ireland to northwestern African waters and Eastern Mediterranean have showed no significant differentiation among samples from the studied areas (Dillane et al., 2000). On the other hand, individuals of *I.*

coindetii from the northern Tyrrhenian Sea (western Mediterranean) and Atlantic Iberian waters were collected at the four year-round seasons in order to compare geographical as well as temporal variation. Results of the study have revealed the presence of a homogeneous population structure, the summer Italian and the spring Atlantic samples being the most divergent among the whole (Martínez et al., 2005b).

Illex coindetii play an essential role in the oceanic system acting as an ‘ecosystem accelerator’, since these are animals with high food intake and high conversion rates thus increasing rates of energy transformation and accumulating high quality protein, available to higher consumers.

In addition, the species has an important commercial value -especially over the last decade- in many areas of the European waters such as the French and Iberian coasts as well as the Mediterranean. Even if it has been a research targeted species and a rich literature provides adequate information, further detailed studies of the life history, and particularly the influence of oceanographic factors, are required towards a sustainable management of its resources over the European Seas (CEPHSTOCK, 2005).

4.2. Landings and CPUE

Illex coindetii has an increasing fisheries value, and represents a valuable resource in some areas of its distribution range due to the amount of catches (e.g. Jereb and Ragonese, 1995). The species is usually sold with the related ommastrephids *Todaropsis eblanae* and, more occasionally, with *Todarodes sagittatus*. For this reason, official statistical data on the landings of the single species are not available (Table 5). Although separate statistics are not reported, the annual catch for ommastrephids in the European waters over the last decade ranges from 3.000 to more than 7.000 metric tons (Anonymous, 2004).

The high inter-annual variation in ommastrephid landings is one of the characteristics of the ommastrephid fisheries throughout the Mediterranean and the Eastern Atlantic (e.g. Stergiou, 1989; Sánchez and Martin, 1993; González *et al.*, 1996c; Sánchez *et al.*, 1998).

Table 5. Total annual cephalopod landings (in tonnes) in the whole ICES area separated into major cephalopod species groups. Groups species of short-finned squid (*Illex coindetii* and *Todaropsis eblanae*), European flying squid (*Todarodes sagittatus*), neon flying squid (*Ommastrephes bartrami*) and occasionally a variety of species belonging to different decapod cephalopod families are sold and are not separated out in the official statistics. Among them *I. coindetii* is the most important commercialised ommastrephid.

Cephalopod group	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Cuttlefish	21073	16424	20497	20572	27950	22711	20834	24661	15196	4538
Common squid	9159	7736	9323	8423	10734	8379	7474	8739	6275	3202
Short finned squid	5529	4238	2508	1590	10972	2387	1233	959	2066	582
Octopods	16453	11442	12836	12223	13213	17884	8981	13335	18399	10366
Total	52213	39841	45165	42808	62870	51361	38522	47694	41936	18689

A marked seasonality in trawl landings of this commercial category was evidenced; this is variable through the range of distribution: peaks in the summer months were showed in the northern Tyrrhenian sea (western Mediterranean - Belcari et al., 1998), while raised values in landings during winter and spring were recorded in the Southern Celtic Sea and Bay of Biscay (NE Atlantic - Arvanitidis et al., 2002).

The total abundance of *I. coindetii* in Central Eastern Atlantic waters is low and does not surpass $0.5\text{--}30\text{ kg h}^{-1}$. Catches are rather higher off the coasts of Sierra Leone, Liberia, Ivory Coast and Ghana at depths up to 700 m. Off Anglola, the catches may reach $0.2\text{--}0.5\text{ t h}^{-1}$ and sometimes, when squid concentrations are high in the area, a target fishery is organised and daily catches up to 3-10 t are possible (Sánchez et al., 1998).

4.3. Recruitment and Environmental Variability

Most of the commercially important species of cephalopods have a short life cycle, grow rapidly to maturity, spawn once at the end of their life, are ecological opportunists and have labile populations consisting of only one or two generations of animals. They also show well-known year-to-year fluctuations in abundance over large spatial scales. These oscillations are widely believed to be caused, to a greater or lesser extent, by the influence of environmental conditions on early life phases that have a major effect on recruitment and, later, on the biomass that can be harvested. Hence we expect that it may be possible to forecast cephalopod abundance based on environmental conditions. *Illex coindetii* biological indices have been correlated with different environmental variables, such as sea surface temperature and Chl-a. These factors and food availability influenced growth rates, spawning season, reproductive peaks, maturation rates, recruitment and other biological factors (Arvanitidis et al., 2002). Besides, different correlation patterns also suggest high levels of environmentally driven flexibility of the life cycle of *I. coindetii*. Large variation in landings (Sánchez et al., 1998) could be attributed to the flexibility of the species life cycle.

In the north-eastern Atlantic, the reproductive life cycle of this species is coupled to the coastal wind-driven upwelling, in such a way that females spawn during spring and summer months, during the upwelling season and hatching takes place from late summer to early autumn.

In this area, based on research surveys undertaken from the 70's to early 90's, *I. coindetii* seem to appear in the late 80's (González et al., 1996c). Actually, the explanation of the appearance of this species in higher abundances during 1987 is unknown but it coincided with a particularly favourable upwelling season that year (Lavín et al., 1991). It is not clear if this species colonised this area from southern or northern waters, where the species were cited in the past.

The opportunistic characteristics of this species could also favour the colonization of Galician waters during a period of decreased abundance of hake, which occupied the same ecological niche. However, it is very difficult that this is the only explanation of the massive increase of *I. coindetii* biomass in Galician waters, which should be influenced also by favourable oceanographic conditions during that period.

4.4. Management and Stock Assessment

Generally, there is no analytical assessment or fishery forecasting carried out on a regular basis for *Illex coindetii*. There are no formal reference points against which to assess stock status, which is therefore usually inferred from trends in landings time-series. Management of cephalopod fisheries tends to be at a national or local scale, in those countries where there are métiers targeting cephalopods, usually artisanal fisheries in clearly defined sea areas and during certain months of the year. Existing regulations relate to permitted mesh sizes or pot designs, designation of closed seasons and setting minimum landing sizes. The management of *Illex coindetii* is also more complicated because it is not a target species within its geographical range, which prevents the establishment of specific management plans or measures.

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Chapter III

***Illex illecebrosus*, Northern Short-Finned Squid**

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Abstract

Short-finned squid (*Illex illecebrosus*) eggs and paralarvae are distributed by the Gulf Stream at least from the Florida Straits to oceanic waters south of Newfoundland, with older stages extending inshore and further north, as far as the southern Labrador shelf. Adults feed in the north and migrate south to spawn. Fishery records only go back to 1880, but jigging for cod bait in Newfoundland may have been among the first occupations for Europeans in North America. For a decade starting in 1975, this squid was the target of an offshore trawl fishery that returned nearly a million tons before collapsing, and extensive field and laboratory research during this period made it one of the best characterized ommastrephid species. This chapter includes re-analyses of these data based on new age estimates. Present efforts, focused on monitoring a slow recovery from the longest series of recruitment failures on record, represent a valuable case study of squid recruitment processes.

1. Introduction

The short-finned squid *Illex illecebrosus* (Lesueur, 1821) is associated with fisheries from Delaware Bay to the Labrador Sea, but its range probably extends further south into the Caribbean and Gulf of Mexico and east into the Atlantic. In the northern region it is very common (Lu, 1973); in peak years its biomass has been estimated at up to 3,000,000 t

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(Froerman, 1980). Its economic importance as bait for the Grand Banks cod fishery is probably centuries old and, as Figure 1 shows, records of the inshore jig fishery, prosecuted mainly for this purpose, go back to the 1800's (Mercer, 1973a).

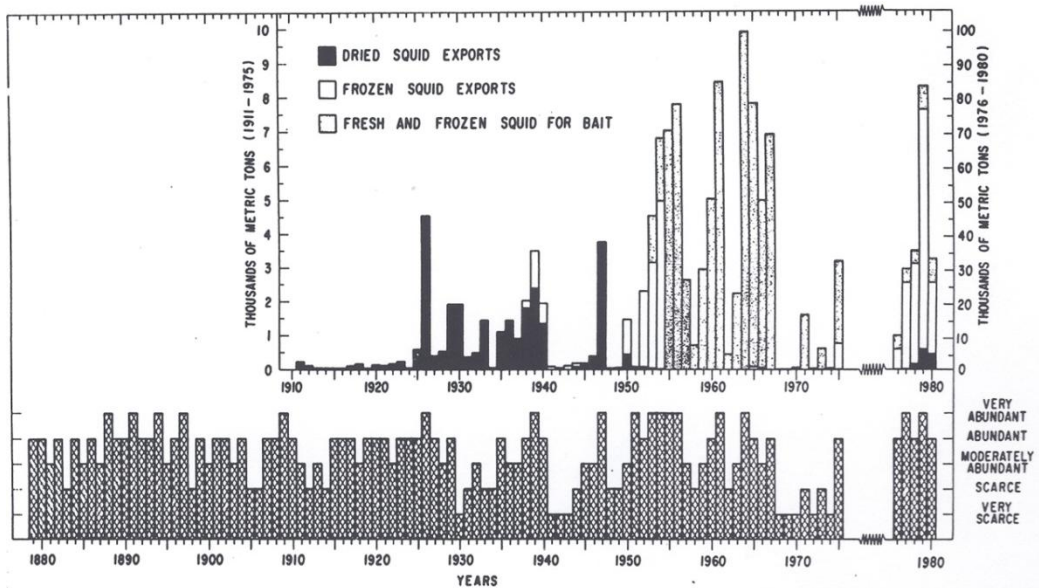


Figure 1. Qualitative estimates of inshore abundance estimates of squid (*Illex illecebrosus*) in Newfoundland, 1879–1980, and a breakdown of inshore catch, 1911–1980 (Note scale change on the catch ordinate for 1976–1980, from Dawe, 1981).

Squires (1957) gave an extensive account of the biology of this squid for the approximately six-month period it spends inshore near Newfoundland. During the late 1970's and early 1980's a greatly expanded fishery for this species provided the impetus for extensive research into its life cycle, including the reproductive and youngest stages. Several summaries of this work have appeared (Aldrich and Arnold, 1991; Balch et al., 1978; O'Dor, 1983; O'Dor and Dawe, 1998; Rowell et al., 1985a), and in recent years efforts have focused on an unusually long period of recruitment failure during the past three decades in Canadian waters (Dawe and Hendrickson, 1998; Hendrickson and Showell, 2010; O'Dor, 1995; O'Dor and Dawe, 1998). This chapter updates previous reviews by summarizing the existing information, including new information on mechanisms that regulate abundance and recent trends in fisheries.

2. Life History Biology

Although the overall distribution limits of *I. illecebrosus* remain unclear, the young stages are associated with the continental edge of the Gulf Stream and subsequently with the adjacent shelf (Figure 2, Dawe and Warren, 1993). Seasonally, large juveniles and adults may occur as far north as the Labrador Sea in summer, but accumulating evidence indicates that abundance near the northern limit varies annually with climatic conditions (Dawe and Warren, 1993; Dawe et al., 2000, 2007). By late autumn, most have emigrated from such northern areas, heading

offshore to greater depths and south. Squid from as far north as Newfoundland emigrate to warm waters on the shelf off the southern United States (Dawe, 1999; Dawe et al., 1981a; Hendrickson, 2004), presumably because eggs fail to develop at temperatures below 12°C.

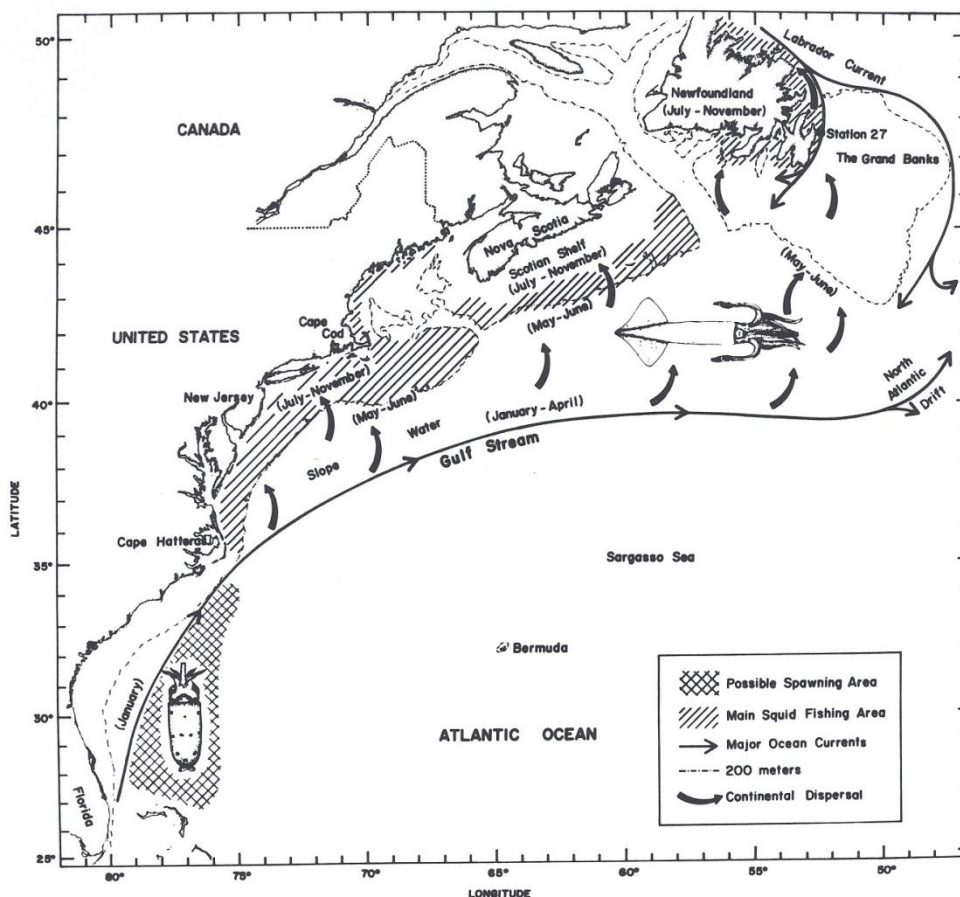


Figure 2. Diagrammatic representation of the life cycle of *Illex illecebrosus* in relation to the main northwest Atlantic Ocean currents and sampling sites (from Dawe and Warren, 1993).

The southward migration may reach a natural block where the high velocity Gulf Stream passes north through the Florida Straits. There are several submersible sightings of large schools of short-finned squids resting on bottom in this area (Voss and Brakoniecki, 1985) and high concentrations in the stomach contents of swordfish there (Toll and Hess, 1981). Near Ft. Pierce, Florida, in late January, 1977, at about 80 m depth, dead, post-spawning specimens of short-finned squid were seen and sampled from a submersible (J.K. Reed, Harbor Branch Foundation *unpubl. data*) at a site where currents would sweep the nearly neutrally buoyant egg masses into the Gulf Stream.

Although these specimens were tentatively identified as *Illex oxygonius* (C.F.E Roper *unpubl. data*), eggs carried north in such masses would release hatchlings that would be transported to the frontal zone between the warm slope waters and the shoreward edge of the Gulf Stream (Bakun and Csirke, 1998) where larval and juvenile *I. illecebrosus* have been

found in greatest abundance (Dawe and Beck, 1985; Fedulov and Froerman, 1980; Hatanaka et al., 1985; Rowell et al., 1985b).

This squid ranges from the surface to depths of 1000 m or more and is taken in waters from 0.5° to 27.3°C (Whitaker, 1980) and from 30 to 36.5 psu salinity (Amaratunga et al., 1980a; Palmer and O'Dor, 1978). Biomass estimates for the Scotian shelf (based on a standardized, annual survey) have ranged over two orders of magnitude (from 2000 t in 1970 to 200,000 t in 1976, Koeller, 1980).

2.1. Characteristics

Externally there is no apparent difference between the sexes until the size at which gonad development begins in males, about 13–15 cm mantle length (ML). However, when the mantle is slit ventrally the two small nidamental glands lying on either side of the mid-line just posterior to the heart can, with practice, be recognized in females >10 cm ML. From June onward, at lengths greater than 13–15 cm, the rate of somatic growth in males decreases so that they are, on average, 5 to 10% shorter than females. The difference in weight is less than that in length because males tend to be slightly heavier at a given length, but there is always considerable overlap in size between the sexes. Differentiation of the hectocotylus begins at the same time the size difference develops. This change may affect either arm R III or L III. Prior to emigration the length of the hectocotylized part may reach 2 cm (Squires, 1957). This species may achieve a maximum length of about 33 cm and a total body weight of 700 g, with females achieving largest sizes.

Length is convenient to measure and often gives a good correlation with age, but weight estimates are more appropriate for relating feeding and catch rates to growth. However, most studies of size and growth have utilized length as the size variable. Total body weight may be estimated from mantle length by applying length-weight relationships. Such relationships vary considerably due to sex, year, month and locality (Dawe, 1988). Lange and Johnson (1979) recommended the composite equation, $W = 0.0481 L^{2.72}$ for relating ML (cm) to weight (g). This equation was derived for adults for use in estimating biomass from length-frequency data, but holds within reasonable limits for all lengths. It predicts a weight of 0.12 mg for a hatchling (which is half the weight of an egg) and is, at worst high by about 50% for large juveniles. Most such fitted equations are out 10- to 100-fold if extrapolated this far.

Weight-at-length also represents an index of condition for use in studies of feeding, energetics or growth. Dawe (1988) found that early-season weight-at-length, and seasonal change in weight-at-length, were related to the prevalence of fish in the short-finned squid diet at Newfoundland.

2.2. Age and Growth

Growth rates can be determined from changes in length over time if there is clear evidence for population homogeneity, if the age of individuals is known or if growth increments can be directly linked to time (Bizikov, 1991). Early analyses assumed that local concentrations of this species were homogeneous.

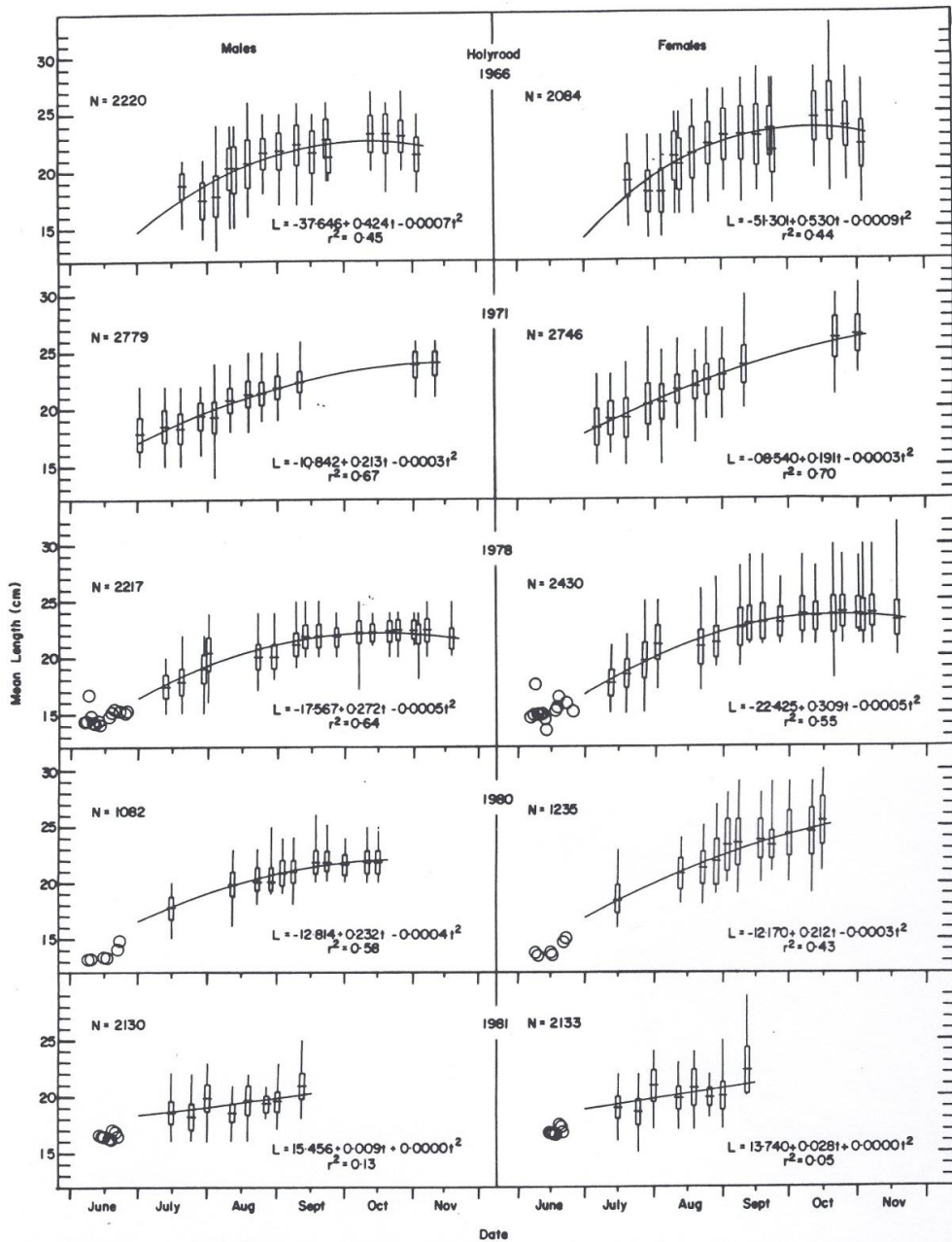


Figure 3. Annual variation in seasonal trends of mantle length for both sexes of *Illex illecebrosus* from the commercial jig fishery in Newfoundland waters. Box and whiskers show mean, SD and range. Circles indicate bottom trawl data from the Grand Banks slope, not included in quadratic models (O'Dor and Dawe, 1998).

This assumption for the Scotian shelf (Amaratunga, 1980a) and Newfoundland (Squires, 1967; Beck et al., 1980) was based on the observation of unimodal length-frequency distributions with length increasing consistently through the year. This is not the case in the south where a second mode suggests a second breeding period (Mesnil, 1977; Lange, 1981; Coelho and O'Dor, 1993).

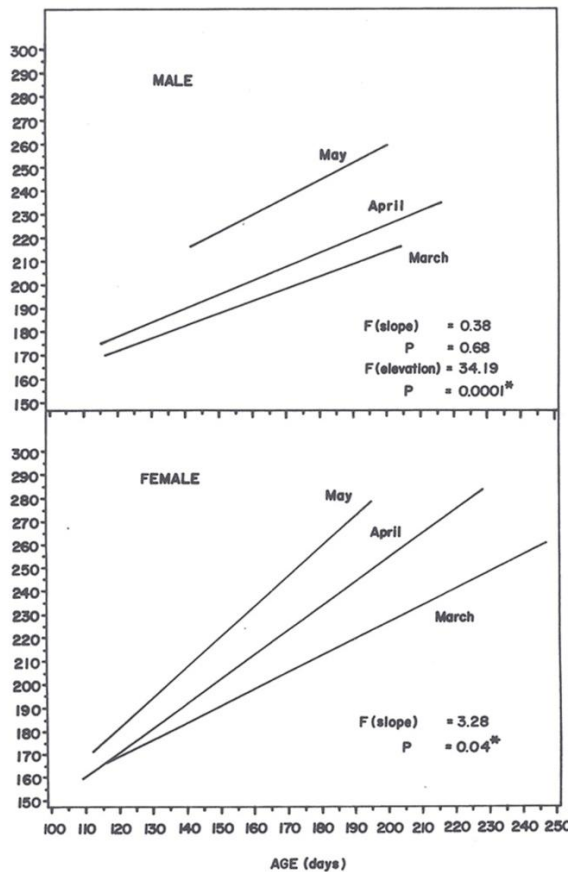


Figure 4. Mantle length at age for *Illex illecebrosus* in Newfoundland waters in 1990 separated by sex. Linear regressions show size dimorphism and different growth patterns between sexes, with progressive increases in growth rates over the season for individuals hatched in different months (Dawe and Beck, 1997).

Early growth studies from Newfoundland (Squires, 1967) and the Scotian shelf (Amaratunga, 1980a) were based on modelling seasonal progression in length using the von Bertalanffy growth model.

However a general quadratic model is more appropriate as a descriptive model because it accounts for the observed late-season decrease in length (Figure 3). Such length-based models suggested that growth in length continued at about 1.5 mm d^{-1} , as suggested for juveniles.

The apparent decline in growth rate from July to September was thought to be due to limited food supply. The apparent asymptotic or late-season negative growth was attributed to emigration of the largest squid. The few unusually small squid found in late winter and early spring were considered stragglers.

More recent studies have been able to utilize data on squid age or growth history determined from examination of statoliths or gladii, respectively (Arkhipkin and Perez, 1998; Perez and O'Dor, 1998, 2000). One such study, based on statolith ageing at Newfoundland, showed that length-based models are not appropriate for describing growth because there was constant interchange within the local population (Dawe and Beck, 1997).

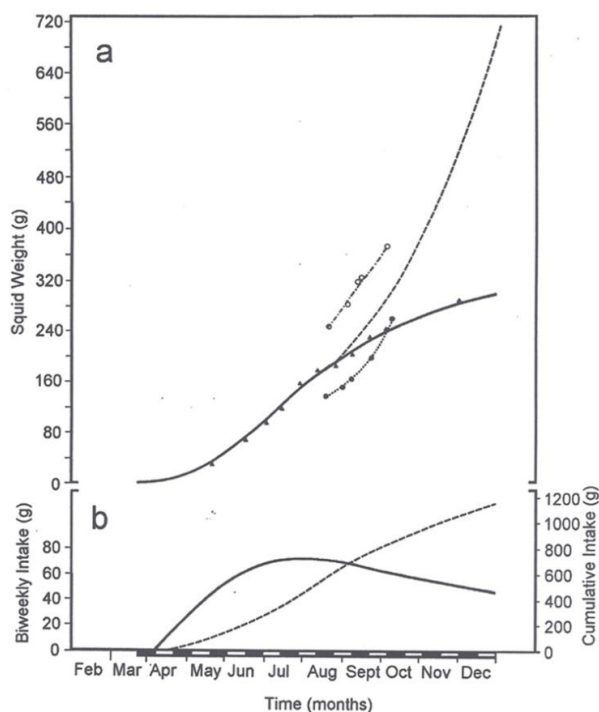


Figure 5. (a) Seasonal weight changes in wild and captive *Illex illecebrosus*. triangle = wild caught squid, 1977; filled circle = a captive population fed *ad libitum* on fish, 1978; empty circle = a single tagged captive. The dashed line projects the weights of the wild population, if they had continued growth at the rate of the captives. (b) Food consumption for an average squid estimated from the sizes of the wild population and the feeding rate/growth rate relationship seen in captives (solid line = bi-weekly consumption, dashed line = cumulative consumption). Note that these calculations assumed a stable wild population and underestimate the requirements of cycling migrant squids. (From O'Dor et al., 1980a).

As Figure 4 shows, growth in length did not decline but was linear throughout the season for animals hatched in the same month. Such rapid seasonal growth, in relation to earlier length-based estimates agreed generally with observations of growth in captivity better than field observations (Figure 5a, O'Dor, 1983). Age-based estimates showed that growth varies greatly among individuals and with time of hatching (Dawe and Beck, 1997). While such (within-study) relative differences in individual, seasonal or annual growth rates are valid, Gonzalez et al. (2000) showed that absolute age estimates may be biased by method of statolith age determination. Accordingly, they advised caution in comparing between studies of age and growth that are based on differing methodologies or age readers. A more recent approach to studying growth performance has been to model weight-at-length (condition) as a function of age (Ragonese et al., 2003). While this method may also be affected by bias in statolith age determination, it offers advantages above traditional size-at-age modelling, including concurrent use of two size metrics, reduced effects of sampling bias, and avoidance of theoretical constraints regarding the form of growth in absolute size. This approach provided comparable or superior model fits when compared with traditional size-at-age models.

2.3. Maturation and Fecundity

Sexual maturation does not occur concurrently between the sexes. Males begin to mature in summer and achieve advanced stages by late fall, whereas females show little evidence of maturation during the fishing season. A commonly used male maturity index has four stages: 1) Immature - all male ducts transparent; 2) Maturing I - thin white mid-lateral streak in spermatophoric organ; 3) Maturing II - vas deferens thick and creamy white; 4) Mature - spermatophores in spermatophoric sac (Mercer, 1973b). In routine use 1) and 2) have been combined (Amaratunga and Durward, 1979). There is a need for a better definition of 'mature' because observations of mating behaviour (see below) make it clear that males are not functionally mature until they have produced a thousand or more spermatophores (O'Dor et al., 1980b). However, spermatophore counts *per se* are not useful since they change with mating. Spermatophore length which tends to increase with squid length (Squires, 1957) and the proportion of arm length hectocotylyzed (Haimovici et al., 1998; Schuldt, 1979) have been examined (Coelho et al., 1985), but no satisfactory relationship has yet been found.

Female *I. illecebrosus* emigrate from fishing areas before maturing so that many details of maturation are known only from studies of captives which advance to maturity in 2 to 3 months (Figure 6). Rowe and Mangold (1975) suggested that such rapid maturation in captivity was a result of experimental starvation, and O'Dor et al. (1977) attributed it to lengthened artificial photoperiod regimes.

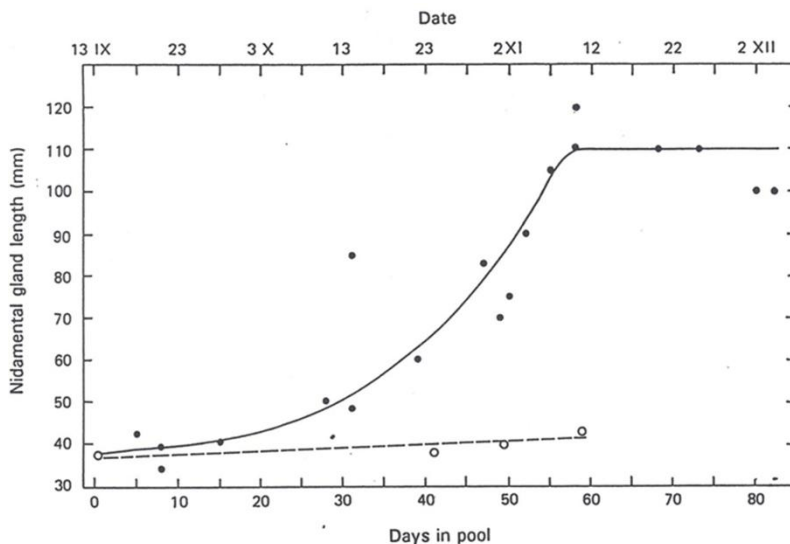


Figure 6. A comparison of maturity, as indicated by nidamental gland length, of wild-caught Nova Scotian inshore female squid (open circles) with captives (closed circles) held over the same period (from O'Dor et al., 1977). Originally presented as evidence for precocious maturation of captives, these data are now interpreted as evidence for population turnover and provide an estimate of natural maturation rates.

This maturation was considered precocious because the maturity of captives was much more advanced than that of the local population in nature at the same time. Since statolith ageing has now shown clearly that the natural population in any location is continually

moving on to be replaced by younger squid (Figure 7, Dawe and Beck, 1997), it now seems likely that the rapid maturation rate of captives is normal.

Although the age structure at a particular locale remains relatively constant throughout the season, due to dynamic migrations, as indicated by the median ages in Figure 7, Figure 8 shows that the animals increase their maturity at a given age (rate of maturation) as the season advances. This is probably because high temperatures accelerate the maturation process (although they do not appear to trigger it, Richard, 1966). Thus increasing maturation rate (and decreasing size and age at maturity) in nature probably reflects the exposure of each successive wave of young squid to progressively higher temperatures as the season advances rather than the progression of a local population. A similar effect of temperature on feeding and growth likely accounts for the increasing seasonal growth seen in Figure 4. This effect of temperature on growth and maturation is reflected in larger body size, and size-at-maturity, of the predominant winter spawning group than of later (spring and summer) spawning groups (Coelho and O'Dor, 1993; Coelho et al., 1994).

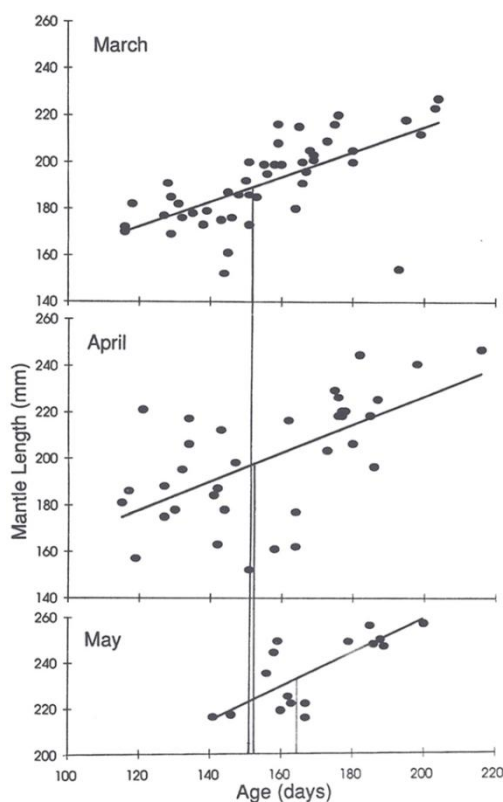


Figure 7. Mantle-length-at-age for male *Illex illecebrosus* in Newfoundland waters in 1990. Linear regressions indicate trends for animals hatched in the three principal months. Although hatching dates advanced by 60 d, median ages at capture (marked by lines dropping to the axis) advanced by only 12 d and the predicted size at this age increased from 190 to 235 mm (adapted from Dawe and Beck, 1997).

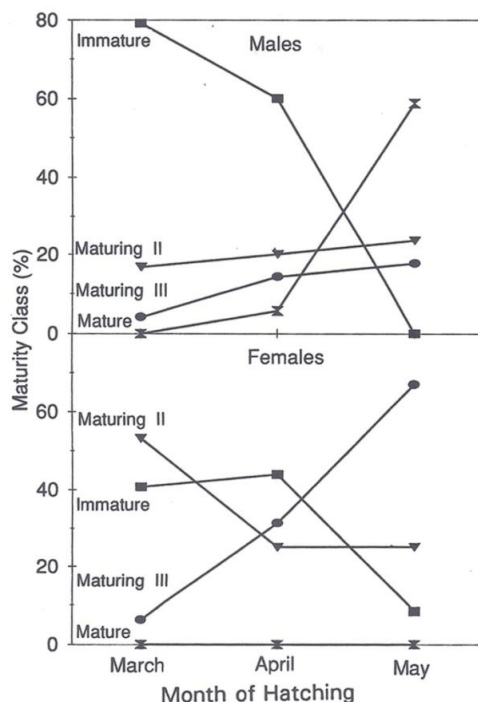


Figure 8. Maturity stages of *Illex illecebrosus* in Newfoundland waters in 1990 for individuals hatched in different months. Late hatching leads to accelerated maturation, since ages at capture typically differ by only a few days (from Dawe and Beck, 1997).

This effect of temperature is also reflected in spatial trends with smaller size and size-at-maturity in southern than in northern areas. Hendrickson et al., (1996) showed that mature (including mated) females caught in a bottom trawl survey in May 2000 on the slope of the southern USA shelf were smaller and younger than immature females typically caught in autumn by the jig fishery at Newfoundland, likely reflecting both seasonal and spatial effects of temperature. The maturation process in females is summarized in Table 1 which relates easily observed morphological features to histologically observed gametogenesis, the ovary to body weight ratio (OW/BW) and the nidamental gland to mantle length ratio (NGL/ML). The NGL/ML ratio is a good index of female maturation for population studies because it is easily determined, continuously variable (and can therefore be easily and meaningfully averaged) and well correlated with other developmental events. Table 1 is based on data from captive *I. illecebrosus*, but gametogenesis and maturation indices are similar for naturally maturing *I. argentinus* (Schuldt, 1979). Available records of mature female *I. illecebrosus* are also consistent with Table 1 (Dawe and Drew, 1981). There is a tendency for segregation of the sexes into separate schools which can produce dramatic shifts in sex ratios as populations turn over (Figure 9). Some inshore populations may be up to 95% female (O'Dor et al., 1980b). Males may predominate (ca. 60%) offshore early in the season, but their proportion may drop to as little as 26% in November (Amaratunga, 1980a). Both the segregation and the shifting ratios may be accounted for by the cannibalistic tendencies of large females.

Table 1. Characteristics of the maturation stages in female *Illex illecebrosus* (Durward et al., 1980)

Maturity Stage	Range of NGL/ML	Range of NGL (mm)	Range of OW/BW	Range of OW (g)	Follicle			Distinguishing Morphological Feature
					Stage ^a	Size ^b (μg)	Dimension ^c (mm)	
I	m≤0.09	11-25	m≤0.0026	0.14-0.90	1	2.1	0.20 x 0.14	NG thin and transparent
II	0.09<m≤0.125	25-35	0.0026<m≤0.0051	0.68-1.60	2	3.5	0.26 x 0.16	NG transparent to translucent ovary granular
III	0.125<m≤0.20	25-60	0.0051<m≤0.015	1.10-5.42	3	11.5	0.35 x 0.25	NG translucent to opaque
IV	0.20<m≤0.35	55-90	0.015<m≤0.09	6.0-30.0	4	-	-	NG white, oviducts forming
V	0.35<m	110-120	0.09<m	50.0-104.0	5	187	0.90 x 0.63	eggs in oviducts

NGL/ML = nidamental gland to mantle length ratio, OW/BW = ovary to body weight ratio.

^a As defined by Selman and Arnold (1977).

^b Calculated using the formula for a prolate sphere, $\frac{4}{3} \pi ab^2$ where a and b are the major and minor semi-axes respectively, and a specific gravity of 1.0. These values are lower by up to one-third than previously published values (O'Dor 1983, Durward et al., 1980), as the published values were incorrectly calculated using equations for oblate spheroids. This increases the fecundity estimates given in the text.

^c Dimensions refer to major and minor axes; measurements of follicles fixed in Bouin's solution.

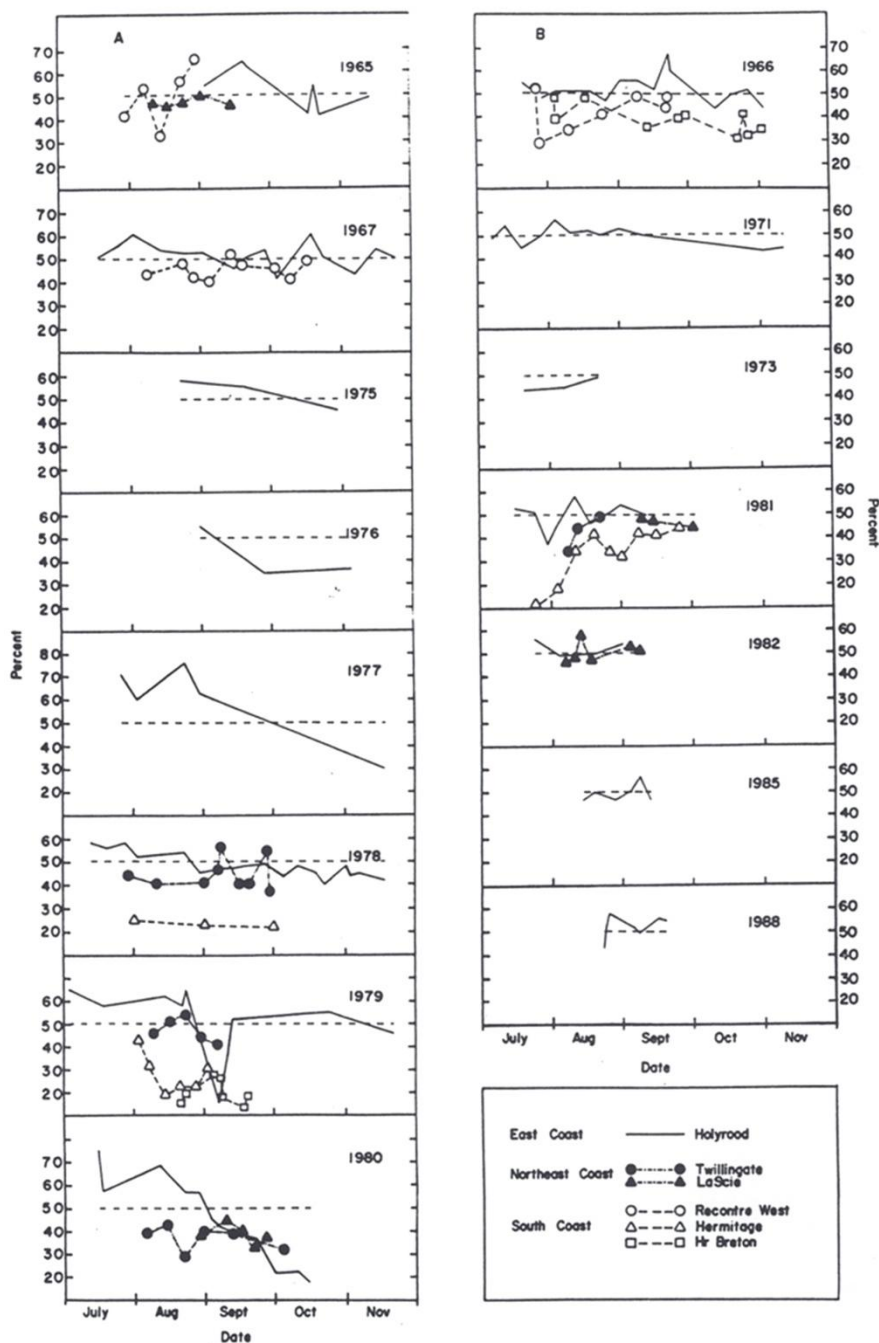


Figure 9. The percentage of male *Illex illecebrosus* varies dramatically with location, season and year. Schools segregate by size and sex, probably because of the prevalence of cannibalism. (O'Dor and Dawe, 1998).

As noted above, males begin to invest energy in gametes earlier and are outgrown by females of the same age. Either cannibalism or early emigration of mature males to avoid it could produce the changes in sex ratios.

Egg numbers are the most commonly used estimator of fecundity, but this is valid only if the fertilization rate is high. Both the changing sex ratio and laboratory records of low fertilization rates suggest that males are potentially limiting in this species. Final egg size is independent of body size, but egg numbers are higher in larger squid. The oviducts of captive females held without males contained eggs amounting to 23% BW at death with little ovary remaining, equivalent to about 1200 eggs per gram BW. When males are present, mating and spawning often occur before all of the ovarian eggs are finished. Females usually die shortly after spawning (O'Dor et al., 1980b), suggesting that actual fecundity may be considerably less than the maximum, unless the sexes are segregated in nature. Captives also rarely exhaust their oviducal egg supply, so a reasonable guess at the spawning fecundity of a typical 400 g female may be 200,000 eggs. Low fertilization and hatching rates may decrease it further.

2.4. Mating and Spawning

The sex ratio may be a determinant of spawning success and fecundity because males appear to be the initiators of mating behaviour (O'Dor et al., 1980b). Figure 10 summarizes an experiment in which two schools of squid were held in a 15-m pool for several months. The pattern observed suggests that when a male is 'fully mature' (precisely what this means remains unclear, Coelho et al., 1985) it will mate with several females. With only one exception mated females were vitellogenic (stage IV) and with only two exceptions they had oviducal eggs present (late stage IV or stage V). This selectivity may reflect an element of female receptiveness since some females resist. Only one or two brief mating encounters have been observed despite extensive efforts, indicating that courtship in *I. illecebrosus* is likely much less dramatic than that described for loliginids (Arnold, 1962; Drew, 1911; Fields, 1965).

Spermatophores are transferred to the inside of the mantle cavity near the oviducal gland, and attached to the mantle, gills or the gland itself during a copulation in which the male grips the female from below (as in *Loligo*, e.g., Figure 1, Plate 1 in Drew 1911) judging from the sucker scars on the dorsal mantle of mated females. Our observations suggest mating takes only a few seconds and does not involve the long rituals common in *Loligo*. The discharge of the sperm is not immediate, however, and intact spermatophores have been taken from captive females up to five days after the death of the last male in a captive school. There are no oral spermathecae in *I. illecebrosus*, and the retention of sperm in the attached spermatophores is the only known means of sperm storage (Hamabe et al., 1974). How long sperm remains viable is unknown. Implantation of the spermatophores is the probable stimulus for spawning which seems to follow within a few days of mating. Two types of spawning have been observed in captivity, both occurring in the afternoon. Two females have been observed spawning on the bottom in a modified 'resting position' (Bradbury and Aldrich, 1969) where the usual cryptic pattern is replaced by a stark pattern of sharply contrasting dark bands (near the lip of the mantle, the fin tip and the arm tips) on a white background. While resting on the bottom both animals made strong, rapid mantle contractions (42 min^{-1} vs. 35 min^{-1} at rest). These contractions did not move the animal suggesting that the funnel was closed or blocked. Mechanical activity presumably mixes ova from the oviducts, gelling agent from the nidamental and oviducal glands and broken spermatophores with water to form the substance of the egg mass.

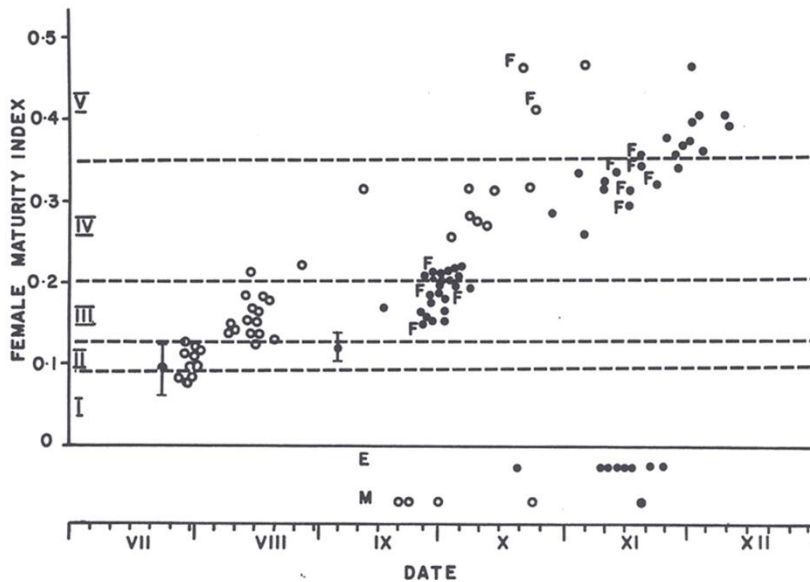


Figure 10. The progress of female sexual maturation and related events in two schools (open vs. closed circles) of *Illex illecebrosus* held in the same tank in 1979. The circles with bars indicate the initial means and standard deviations of the maturity indices (See Table 2, NGL/ML) at the time of capture; other circles are for individuals measured at death. The letter F indicates spermatophores were present in the mantle. Egg masses were noted at the dates indicated (E) and the death dates of males are indicated (M) (from O'Dor et al., 1980b).

This gel was pumped out between the arms to accumulate in front of the female as a large mass on the bottom similar to those described by Hamabe (1963) for *Todarodes pacificus*. In captivity, single *I. illecebrosus* females produce several (six is the maximum count) of these nearly spherical egg masses up to one metre in diameter. Ten to fifty thousand eggs per mass is typical, but the largest may contain up to 100,000 (Durward et al., 1980).

One *I. illecebrosus* has also been filmed spawning in midwater in a large pool (O'Dor and Balch, 1985). This squid apparently preformed a concentrated gel mixture in the mantle while resting on bottom and then inflated it in 1 to 2 min while hovering in midwater using rapid fin movements. Frame-by-frame analysis shows that the egg mass swells rapidly and becomes more tenuous, like a balloon full of gelatin being inflated with hot water. The mass is held in outstretched arms and sinks when released.

2.5. Egg Balloons and Embryonic Development

Although these gel balloons are slightly denser than the seawater incorporated into them, changes in water density of as little as 0.05 kg m^{-3} have lifted balloons off the bottom (O'Dor and Balch, 1985). Because of their large size and lack of internal convection, thermal equilibration in such masses is slow and chemical equilibration even slower. Balloons made of warm surface water would sink very slowly into cooler, denser water at depth, allowing time for the rapid development of these small eggs. Balloons formed in the lower salinity surface water of the Gulf Stream would become buoyant as they sank into its higher salinity core.

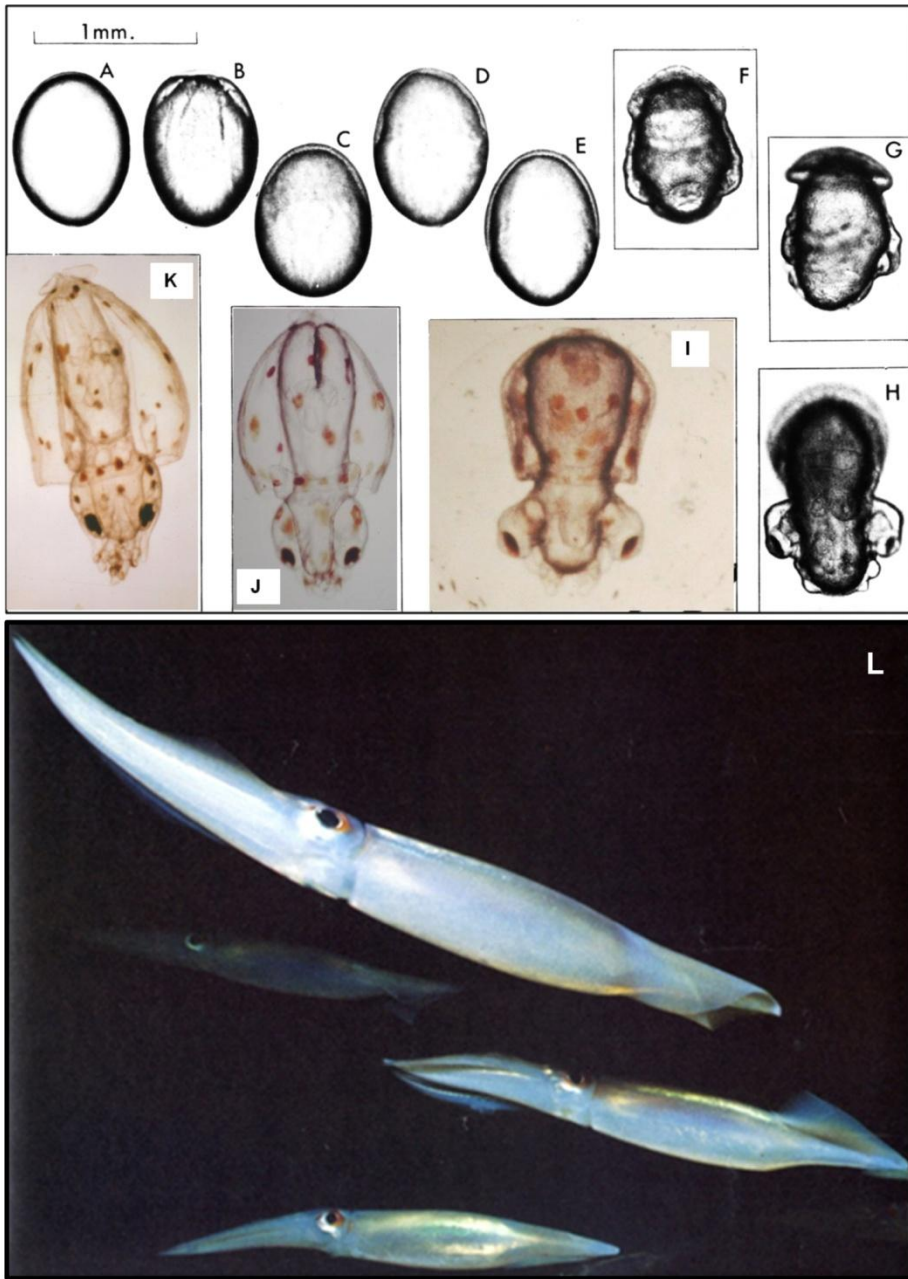


Figure 11. Egg development in *Illex illecebrosus* at 22°C. A = unfertilized egg, B = fifth cleavage, 5 h, C = stage III (Naef 1921-1923), trilaminar blastoderm, 1/3 cellulated, 24 h, D = stage V, 1/2 cellulated, 2 d, E = stage VII, cellulation nearly complete, eye and mouth placodes visibly thickened, 3 d, F = stage IX, mantle development begins, yellow pigmentation of eyes, chorion expanding, 4 d, G = stage XI, arm primordia I, II, III, IV (tentacles) visible, chromatophores forming on mantle, 5 d, H = stage XIII, mantle reaches mid-line and begins to contract, funnel tube complete, 6 d, (I) stage XV, expanded chorion, eye lens, and sucker primordia visible, eye stalks and fins prominent, 7 d, J = stage XVII, eyes move inward as yolk sac elongates and bifurcates, tentacles fused, mantle covers funnel, 8 d, K = stage XX, yolk sac being consumed; ink sac, fins and buccal mass functional, extensible proboscis, 9 d. (from O'Dor et al., 1982). L) Adult *Illex* in Dalhousie's Aquatron Pool Tank where the egg masses were produced. Image from Bob Seple, Fisheries and Oceans Canada.

Even balloons formed on the bottom could be lifted up by storms or shifting currents that cause local increases in water density or even by isopycnal changes in one variable. A gel made of cold, low-salinity water would become less dense as heat was transferred from isopycnal, warm, high-salinity water. Because heat transfer is faster than salt diffusion, the warm, low-salinity water in the gel would become less dense. Warming can also cause supersaturation, forming minute gas bubbles in the gel which would produce floatation. Ammonium ion production from protein breakdown during development could also contribute to increased buoyancy.

The only published record of eggs of the genus *Illex* from nature is of a large floating mass from the Mediterranean near Naples (Naef, 1928) which was later identified as *Illex coindetii* (Boletzky et al., 1973). The rarity of reports of floating squid masses in general (Clarke, 1966) suggest that their buoyancy features may isolate them from both benthic and planktonic predators in midwater pycnoclines or currents. Capturing such egg balloons in midwater is exceedingly difficult, even in captivity with optimal visibility (Balch et al., 1985); the pressure wave in front of a plankton net easily deflects them and they would certainly be destroyed by larger mesh bottom and midwater trawls. Thus they are not only difficult to collect as specimens but also probably hard to eat!

Finished eggs weigh 200 – 250 μg each and are ovoids ranging from 0.9 by 0.6 to 1.0 by 0.8 mm with a distinct micropyle at the larger, animal pole. As an aid to identification of egg masses, Figure 11 provides a brief description of embryonic development. Premature hatching may occur after as little as 10 days at 13°C, but full development requires 16 days at this temperature (O'Dor et al., 1982). Laboratory experiments indicate that the rate of development increases with temperature up to at least 26°C where development requires only 6 days (Balch et al., 1985). The minimum temperature at which normally spawned eggs will develop is about 12°C (O'Dor et al., 1982). At 7°C no development occurs; although eggs fertilized at this temperature will develop if the temperature is raised. Eggs developing at 17°C degenerated when the temperature was lowered to 7°C. The large egg balloons protect the eggs from rapid temperature changes which can cause abnormal development.

2.6. Spawning Area and Season

The observations of midwater spawning dramatically increase the number of potential spawning sites and the complexity of discriminating stocks. Spawning could occur and produce normal development in the Gulf Stream or anywhere in the north Atlantic central waters (O'Dor and Balch, 1985). Even egg masses formed at temperatures too low for immediate egg development could be 'activated' by contact with warmer water. For example, winter temperatures in the shelf waters are too low for development, but where these southward moving coastal waters meet the Gulf Stream south of Cape Hatteras there is intense mixing and production of warmer slope waters where normal development could proceed (Pickart, 1994; Trites, 1983).

No *I. illecebrosus* egg masses have ever been found in nature, so spawning seasons were traditionally estimated from squid size and the timing of advanced male maturity stages, as well as the appearance of paralarvae in the plankton (Dawe and Beck, 1985; Lange, 1981; Lu and Roper, 1979; Hatanaka et al., 1985; Rowell et al., 1985b; Squires, 1957, 1967). All such

data suggest that the main spawning period is in winter. Ageing techniques represent a much more powerful approach, but only a few such studies have provided estimates of hatching date (Dawe and Beck, 1997; Dawe et al., 1985).

There are relatively few records of advanced maturity stages for female *I. illecebrosus* in nature because the fishery is concentrated on immature populations on their feeding grounds. The records of fully mature females from spring and early summer cruises (Mercer and Paulmier, 1974; Lipinski, 1979; Squires, 1967; reviewed by Dawe and Drew, 1981) and of maturing specimens from winter surveys (Amaratunga et al., 1980b), are so few that they seem unlikely to represent the major spawning population. A 1979 bottom trawl survey of the continental slope from Georges Bank to Cape Canaveral found relatively large concentrations of *I. illecebrosus*, including squid up to 34 cm ML and nearly fully mature females in the 300 to 1000 m zone during October and November (Rathjen, 1981). Until recently only two records of mated females from nature existed (spermatophores present in the mantle cavity); one in July from an unreported site between Cape Hatteras and the Scotian shelf (Hamabe et al., 1974), and one in June from Browns Bank (Mercer and Paulmier, 1974). However Hendrickson (2004) reported the capture of 24 mated females during a May 2000 bottom trawl survey. These females were caught on the shelf slope in the mid-Atlantic bight, north of Cape Hatteras, and it was deduced that this represented a spawning area. However that seems unlikely given the absence of any spent females, and the evidence that spawning generally occurs south of Cape Hatteras. It is more likely that these spring-spawning mated females would move further south and offshore to spawn within the Gulf Stream.

If spawning occurs predominately in late winter at an appropriate site, the egg masses might be picked up by or rise into the Gulf Stream as they develop and be delivered back to sites along the shelf edge just in time to meet the next spring bloom. At 7 km h^{-1} , the average speed of the Gulf Stream, 10 days would allow an egg mass to move from almost any point on the coast to any other.

3. Ecology

3.1. Effects of Ocean Climate Variability

Recent studies have shown that this species is highly adapted to physical and biotic ecosystem variability. (Dawe et al., 2000, 2007). Variation in population abundance is closely related to variability in multiple interacting ocean climate processes. Dawe et al. (2000) showed that squid abundance is positively related to a favourable oceanographic regime associated with a negative North Atlantic Oscillation (NAO) index (weak winter northwesterly winds), high water temperatures off Newfoundland and a southward shift in the position of Gulf Stream and the boundary between the shelf waters and the offshore slope waters. In addition, decreased meandering of the Gulf Stream appears to promote increased abundance, probably through enhanced downstream transport of squid. Such ocean climate relationships with squid indices are believed to reflect effects of broad-scale winter atmospheric circulation patterns on Gulf Stream dynamics, which largely regulate year-class strength of the dominant winter-spawning group early in life. This is highly adaptive in that environmental conditions which promote strong year-classes also favour population

expansion through expedient advection of young stages and a suitable oceanographic regime in the northern-most area. Individuals of the broadly distributed winter-spawning group are strongly selected for large body size because near maximum growth and delayed maturation may be necessary to survive the lengthy spawning migration and complete the life cycle. In direct support of this strategy, it appears that squid body size and physical condition (Dawe, 1988) at Newfoundland are directly positively related to recruitment magnitude, indicating early peak spawning or rapid growth rate in warm years of high abundance.

It has been hypothesized (Dawe et al., 2007) that there is a limited carrying capacity for squid and the southern (USA) region approaches its relatively stable limit each year. The carrying capacity near the northeastern limit of distribution, in Canadian waters may be much more variable with higher capacity in warm years. Furthermore, short-finned squid shares its habitat with a sympatric long-finned squid (*Loligo pealei*) in the southern (USA) region. A recent study showed that these species share habitat and a common niche through opposing responses at the population level to environmental variation, such that their populations vary inversely (Dawe et al., 2007). The neritic long-finned squid is associated with higher bottom temperature conditions than is the oceanic short-finned squid on the USA shelf. (Brodziak and Hendrickson, 1999). Strong atmospheric forcing (positive NAO) generally results in high bottom temperatures in the southern area, favourable for long-finned squid, whereas weak atmospheric forcing (negative NAO) results in southward displacement of the Gulf Stream and associated fronts as well as warm bottom temperatures at the northern extreme, conditions favourable for short-finned squid.

3.2. Life History Strategy

All available data suggest that longevity for this species is about one year (Dawe and Beck 1997; Dawe et al., 1985; Squires, 1967), although this is probably somewhat variable (Coelho et al., 1994; Squires, 1967). Maximum age estimated at Newfoundland in one limited study did not exceed 250 days (Dawe and Beck, 1997), whereas *Illex argentinus* of about 360 days of age (Arkhipkin and Laptikhovsky, 1994) have been collected on the Patagonian shelf. This difference is probably related to the remote location of the northern-most fishery area for *I. illecebrosus* (Newfoundland) from its spawning area, relative to that for *I. argentinus* (Coelho and O'Dor, 1993; Coelho et al., 1994; O'Dor, 1998).

Spawning likely occurs throughout the year with some seasonally intense periods. The most intense spawning is apparently in winter (Squires, 1967), with a secondary peak in summer (Coelho et al., 1994; Lange, 1981). These seasonal peaks appear to be adaptively timed so that juveniles may avail of major seasonal productivity peaks in spring and autumn respectively (O'Dor, 1998). It appears that the usually most abundant winter-spawned squid are the most broadly dispersed, supporting fisheries in northern-most areas when climatic conditions are suitable, whereas summer spawners remain in closer proximity to the spawning grounds (Coelho and O'Dor, 1993; Coelho et al., 1994; O'Dor, 1998). Abundance of winter-spawned squid is highly variable in most northern (Canadian) fishery areas, whereas it is more stable (perhaps serving as a 'reserve') in the southern-most (USA) area.

An annual species such as this must be capable of adapting to an annually variable climate. This is apparently accomplished by maximizing the distribution of both reproductive effort over time and individuals over space (Coelho et al., 1994). With limited food supply,

cannibalism provides the final energy reserve for the spawning migration (O'Dor, 1998). It has been suggested that the major winter group may become depleted and it would subsequently 're-evolve' from other seasonal spawning groups. An alternative possibility is that this major group does not become depleted because its southern 'reserve' is relatively stable; it is probably not dispersed to northern fishery areas when the total population is low and the climate is unfavourable (Dawe and Warren, 1993; Dawe et al., 2000, 2007). This major seasonal group may simply shift its time of peak spawning with climatic variation. It is presently unknown whether the March to May peak hatching months of squid sampled in 1990 at Newfoundland (Dawe and Beck, 1997) represented the usual peak hatching time or, alternatively, whether it reflected delayed spawning in a year of low squid abundance and an unfavourable climate.

Certain aspects of population structure remain unclear, particularly the processes which cause the late-season decrease in mean length and seasonal decline in the proportion of males in some years. The seasonal decline in prevalence of males may be due to cannibalism by large squid (especially females) or emigration of mature, and presumably large, males. Cannibalism would promote seasonal increase in mean length whereas emigration of males would promote seasonal decrease in mean length of males only. However, the late seasonal decline in mean length is similar between the sexes (Figure 3), and observed age structure in one year showed no evidence of males emigrating before females (Dawe and Beck, 1997).

Cannibalism and male maturation probably affect size distributions and sex ratio, but seasonal decrease in mean length is more likely related to the dynamic interchange within northern fishery areas, as described above. Seasonal length increase is inhibited by the late-season arrival in low numbers in some years of particularly small (and presumably young) squid (Squires, 1957) which likely resulted from late-spring or summer spawning (Lange, 1981; Lange and Sissenwine, 1983). Such late-spawned squid have a limited feeding season available so they reach feeding areas at a young age. They probably grow quickly (Dawe and Beck, 1997) and may mature at a relatively young age and small size. Their arrival in northern areas at a very young age may be related to seasonal variation in physical transport mechanisms or to northward extension of the spawning area during the warmest season (Trites, 1983).

Although these squid may move inshore in pursuit of food, they spend much of their lives on the outer shelf and continental slope. Rhynchoteuthions and juveniles are abundant in the slope water of the Gulf Stream and in the adjacent upwelling regions at times of maximum production such as the spring plankton bloom. As the initial biomass of the bloom is transferred up through various trophic levels the squid grow at a pace which allows them to feed continuously at the level where biomass is peaking. By the time these fluctuations in the food supply have levelled out, the squid, which can eat prey almost as large as themselves (O'Dor et al., 1980a), can manage to take fish several years old. Some squid move inshore in June-July, probably following fish such as herring, mackerel and capelin. Others remain on the shelf where they feed throughout the water column on prey ranging from surface swarming euphausiids (Brown et al., 1981; Nicol and O'Dor, 1985) to bathyal myctophids (Amaratunga, 1980b). They surface at night, feed intensively before dawn and then descend to depths of several hundred metres during the day (Amaratunga, 1980b; Amaratunga et al., 1979, 1980b). Not every squid makes such vertical migrations each day, they probably only do so when hunger drives them there in search of crustaceans which remain their principal food. The surface is both risky, due to the predatory birds and mammals, and energy

expensive; these squid must do work to overcome their negative buoyancy and also have much higher metabolic rates at the higher surface temperatures (DeMont, 1981). The cryptic resting posture is probably an adaptation to the avoidance of benthic predators on the bottom during the day.

The vertical migrations may also be energetically linked to extensive horizontal migrations. Since squid are negatively buoyant like tuna they can save energy by using climb and glide swimming. A squid at the surface near the edge of the shelf may spend several hours and cover many kilometres by gliding down at a flat angle (O'Dor, 1988). Such behaviour, particularly in the presence of favourable currents, could make long migrations much less costly than would be predicted from the cost of steady swimming (Webber and O'Dor, 1986). The precise length of the spawning migration is unknown, but tag recoveries indicate that they can cover distances of over 2000 km (from Newfoundland to Maryland) averaging nearly 20 km d⁻¹ (Dawe et al., 1981a). The direction is generally southward with a clear ontogenetic descent in the autumn as the large squid move into deeper water (Amaratunga, 1981a; Amaratunga et al., 1980a; Dawe, 1999). This scenario would return them to suitable spawning sites at >12°C, as deep Gulf Stream counter-currents provide a push towards suitable areas on the southern shelf (Pickart, 1994; Trites, 1983) and is substantiated by concentrations in deep slope waters (Dawe, 1999; Hendrickson, 2004; Rathjen, 1981).

Limited data indicate a possible nocturnal ascent of juveniles (Dawe et al., 1981b). During the night, 75% of the catch in the first 500 m occurs in the first 100 m while in the day the figure drops to 40 (Amaratunga et al., 1980a). Froerman (1980) has noted, however, that total catchability in the first 500 m during the day is only 25 to 35% of that at night so that differences may reflect net avoidance. The low proportion of juveniles taken with gut contents (13%, Amaratunga, 1980b), is also consistent with a diurnal feeding cycle. Few of these juveniles had identifiable prey items present, but in the larger ones (45–94 mm ML) amphipods, mysids and copepods were common and over half contained fragments of other juvenile squid (*I. illecebrosus*).

3.3. Feeding Ecology and Behaviour

The great variability in size-at-age and growth of individuals may be related to variability in feeding rates (Figure 12). In captivity, feeding hierarchies seem to be established in which some squid take several prey items before others feed at all and a similar situation may exist in nature. Meals of up to 25% body weight (BW) are occasionally taken, but feeding rates in excess of 10% BW per day are not sustained. This rate yields optimum efficiency in conversion of fish weight to squid weight, which may exceed 50% for individuals, giving daily growth rates of over 5% BW. For whole schools, efficiencies are lower by 25% to 35% as shown in Table 2. Feeding rates and growth rates seem to increase with temperature and decrease with weight, but the relationships are not well defined. O'Dor and Wells (1987) examined the interaction of temperature and body size on metabolic rate and feeding rate. The relationships suggest that maintenance food requirements are peaking for large squid at seasonal maximum temperatures of about 15°C in September. In combination with low food availability this could produce declining growth rates.

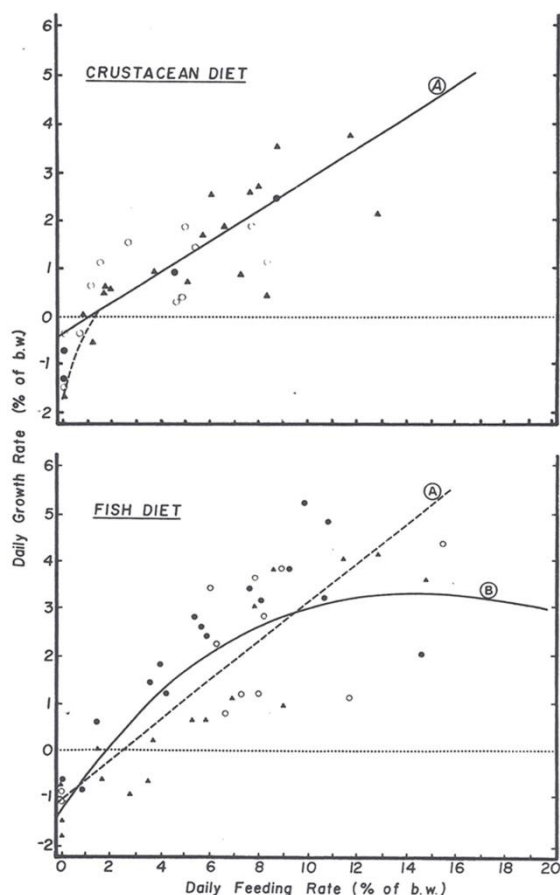


Figure 12. Daily growth (DGR) and feeding rates (DFR) for individual, tagged squid in a school fed ad libitum, twice daily on either crustaceans (*Crangon* sp.) or fish (*Fundulus* sp.). Squid were weighed and diets alternated at 3 d intervals ($\bullet$ = 75–89 g squid, $\circ$ = 90–99 g, $\blacktriangle$ = >100 g). Crustacean diet A: fitted regression ($DGR = 0.32 D \cdot FR - 0.37$, $r = 0.79$, $n = 40$). Fish diet A: linear regression for all observations ($DGR = 0.39 D \cdot FR - 0.99$, $r = 0.79$, $n = 60$); B: $DGR = 0.86 D \cdot FR \exp (-0.069 DFR) - 1.3$ ($r = 0.85$, $n = 60$). Note the high individual variation in feeding and growth rates, as well as food preference. From Hirtle et al., 1981.

This squid plays an important role in the ecosystem as a prey species as well as a predator (Dawe and Brodziak, 1998). The predominance of prey types within its diet changes with the season and ontogeny from crustacea to fish and then to squid. Fish consumption is greatest in summer especially on the U.S. shelf and in Newfoundland coastal waters. Fish is not as prevalent a prey type on the Scotian shelf where the diet tends to shift directly from crustaceans to squid.

In the spring 60% to 70% of the squid examined in each fishing area have food in their guts, but by late autumn only 20% to 25% do. Since digestion requires at least 8 to 12 h and more than 24 h for large meals (Boucher-Rodoni, 1975; Wallace et al., 1981) the average time between meals must be more than a day in autumn. This is consistent with the model calculations shown in Figure 5b which suggest that squid eat more in their first four months than in the next five. However, the assumption that field data represent a stable population is no longer accepted (see below), so the case is certainly overstated.

Table 2. Growth parameters for *Illex illecebrosus* fed *ad libitum* on fish (*Fundulus* sp.) at various body weights and temperatures

Date	Mean Wt (g)	Mean Temp.(°C)	Daily feeding rate (% BW)	Daily growth rate (% BW)	Food conversion rate (%)
28.6.79 - 10.7.79 ^a	104	7.0	5.2	1.3	25
1.8.78 - 7.8.78 ^b	159	9.7	3.6	1.0	29
11.8.78 - 24.8.78 ^b	183	10.3	3.8	1.4	36
25.8.78 – 7.9.78 ^b	232	15.5	6.7	1.9	28

^a Averages for marked individuals (Hirtle et al.1981).
^b Based on feeding and growth of whole schools (O’Dor et al. 1980a).

Fish appears to become a more suitable prey type than crustaceans during summer, probably because of rapid squid growth and the need for progressively larger prey. It appears that physical condition (weight-at-length) of squid at Newfoundland was directly related to the prevalence of fish in the diet (Dawe, 1988).

This suggests that absolute abundance of fish prey or competition for fish prey may have considerable impact upon local squid populations. Similarly, predation by squid could be an important source of mortality in fish populations. Squid at Newfoundland prey first on large, presumably post-spawning, capelin (*Mallotus villosus*) in July and then switch to smaller juvenile fish (predominately gadoids) (Dawe et al., 1997). They resort to cannibalism in autumn as other prey types become depleted, unavailable (Ennis and Collins, 1979; Squires, 1957) or unsuitable (Dawe et al., 1997)

Cannibalism appears to be an important element in the life cycle of this species. In nature it increases as total feeding decreases, and the largest squid are the most cannibalistic (Amaratunga, 1980b; Dawe and Brodziak, 1998).

The same pattern is seen within schools of captive squid where about three days of starvation are needed to induce cannibalism; a single victim may be divided between several cannibals with each getting approximately its maintenance ration (O'Dor et al., 1980a). This would ensure survival of a breeding stock, and would provide an interesting population control since sexual dimorphism makes the smaller males the likely victims. This pattern of cannibalism may also create 'apparent growth' in population studies since selective removal of small animals will increase the average weight even if no individuals grow. A starving population may therefore appear to grow faster than a moderately well-fed one (Arkhipkin and Perez, 1998).

4. Fisheries

4.1. Fishing Areas and Catch Trends

Trends in *I. illecebrosus* fisheries in any of the three fishery areas (Figure 2) have not been reviewed for more than a decade (Dawe, 1981; Dawe and Hendrickson, 1998; Hurley, 1980; Lange and Sissenwine, 1983; O’Dor and Dawe, 1998).

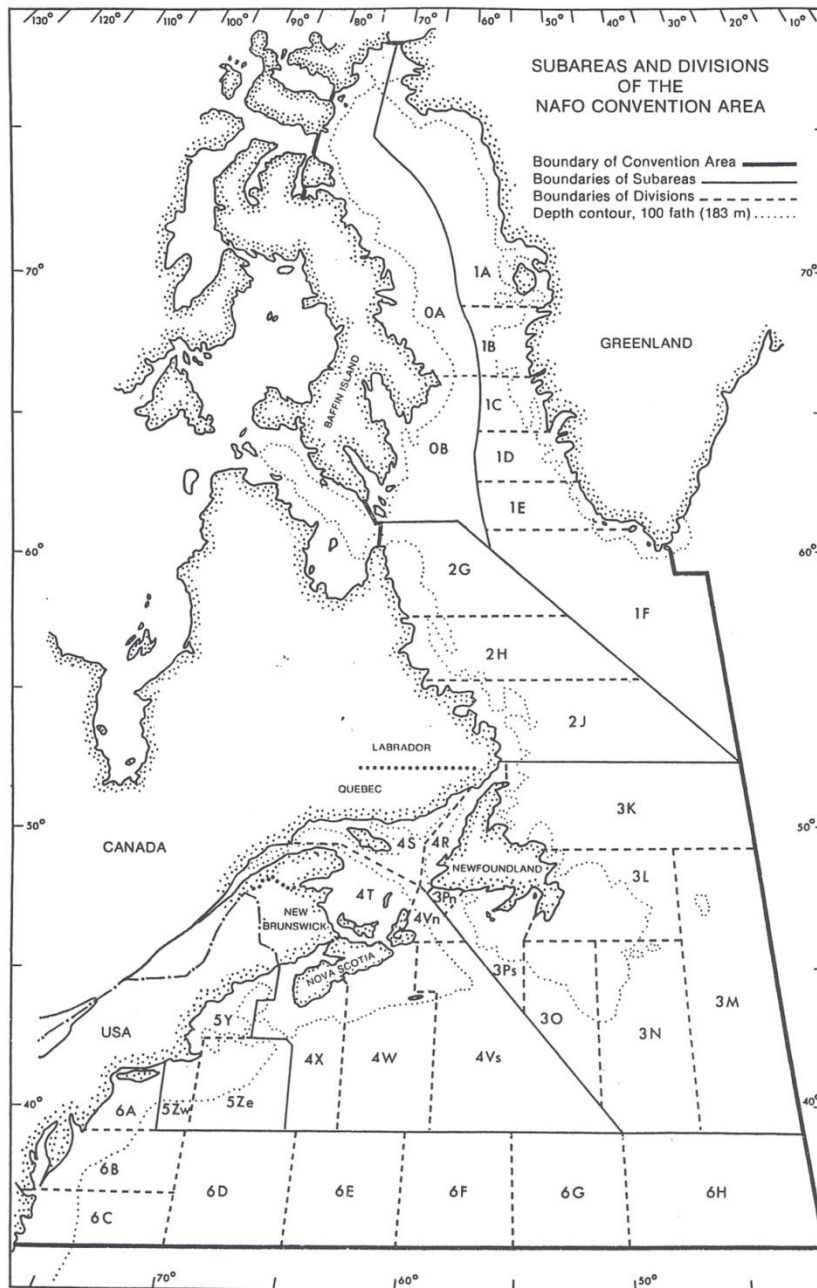


Figure 13. Map of the northwest Atlantic, showing NAFO (and ICNAF) subareas discussed in the text.

The three fishery areas correspond to management areas (Subareas) of the International Commission for the Northwest Atlantic Fisheries (ICNAF) and its successor, the Northwest Atlantic Fisheries Organization (NAFO). These areas (Figure 13) include Newfoundland (Subarea 3), Nova Scotia (Subarea 4), and the northeastern USA (Subarea 5+6).

The oldest directed fishery is the artisanal inshore fishery at Newfoundland (Dawe, 1981; Squires, 1957; Templeman, 1966). This fishery is a passive one, prosecuted very near shore in small open boats. Very little of the annual catch is derived from offshore waters; the

maximum proportion caught offshore was 11% (5,050 t) in 1978. The small offshore Subarea 3 catches are usually taken on the southwestern portion of the Grand Bank and St. Pierre Bank (NAFO Divisions 3PNO, Figure 13). However in some years squid may be distributed to the northern and eastern edges of the Grand Bank as well as on the Flemish Cap (Hurley and Beck, 1979; Vázquez, 1991, 1992). Inshore catches are mostly from the jig fishery, in which multiple barbless jigs are fished in series on monofilament lines. Several lines are usually concurrently fished using hand-operated reels. In certain areas some of the catch is taken using traps. In some years a very small proportion of the catch is derived from Labrador (Subarea 2); these catches are included in the Subarea 3 catch here, for convenience.

Commercial catch data from this fishery date back to 1911 and a subjective ranking of inshore squid abundance at Newfoundland dates back to 1879 (Figure 1). This fishery developed in three stages, related primarily to market developments. Initially, squid were fished mainly for drying (Hurley 1980) and export to China (Figure 1). Annual catches remained below 5,000 t during this period. They increased during the next stage (about 1950–1975), peaking at about 10,000 t in 1964. These larger annual catches were related to the development of a market for squid as bait, for European interests fishing in the northwest Atlantic. A huge market developed in the mid 1970's for squid as food, mainly in Japan, due especially to declining Japanese domestic squid catches. With strong foreign markets for both frozen whole and dried squid, the Newfoundland annual catch increased regularly from 1974 to peak at about 89,000 t in 1979. Annual catches declined regularly since 1979 to only about 5 t in 1983 (Figure 14) due to low abundance of squid. Since 1983 abundance has remained generally low, with peaks of about 4,400 t in 1990, 12,700 t in 1997, and 7,000 t in 2006 (Hendrickson and Showell, 2010). This 27-year period of poor fishery performance at Newfoundland represents the longest period of poor recruitment and low squid abundance in the history of the Newfoundland inshore squid fishery (Figs. 1 and 14). However recent peaks in 1997 and 2006 do not well reflect abundance, as fishing effort was low due to reduced market value and low price in recent years.

In the two more southern fishery areas (Nova Scotia and northeastern USA) the squid fisheries have for more than three decades been predominantly prosecuted offshore using trawls. Trawl fisheries have been mainly by foreign fleets in both areas but with a more prominent domestic component in the northeastern USA fishery than on the Scotian shelf. Squid may be available as early as April in both offshore areas, whereas squid virtually never become available to the inshore Newfoundland fishery before July. Historical catch data date back to 1920 for Nova Scotia (Lange and Sissenwine, 1983; Mercer 1973a). Catch statistics date back to 1887 for the USA total squid fishery (*I. illecebrosus* and *Loligo pealei* combined), and are available by squid species beginning in 1963 (Lange and Sissenwine, 1983; Tibbetts, 1977).

Annual catch at Nova Scotia remained below 800 t during 1920–1968, with the exception of three years (1921, 1925 and 1926) when annual catch levels rose to between 1000 and 2000 t (Lange and Sissenwine, 1983). Catches during that period were mostly incidental from other trap fisheries. Annual catch increased to about 1,300 t in 1970 and 7,300 t in 1971 (Figure 14) due mainly to offshore catches by the USSR and, to a lesser extent, Japan (ICNAF 1978). Further expansion occurred during 1975 and 1976 due to increased recruitment of squid on the Scotian shelf and a great increase in participation by foreign fleets. Foreign fleets participating in this fishery increased from three in 1974 to ten in 1976 (ICNAF 1978).

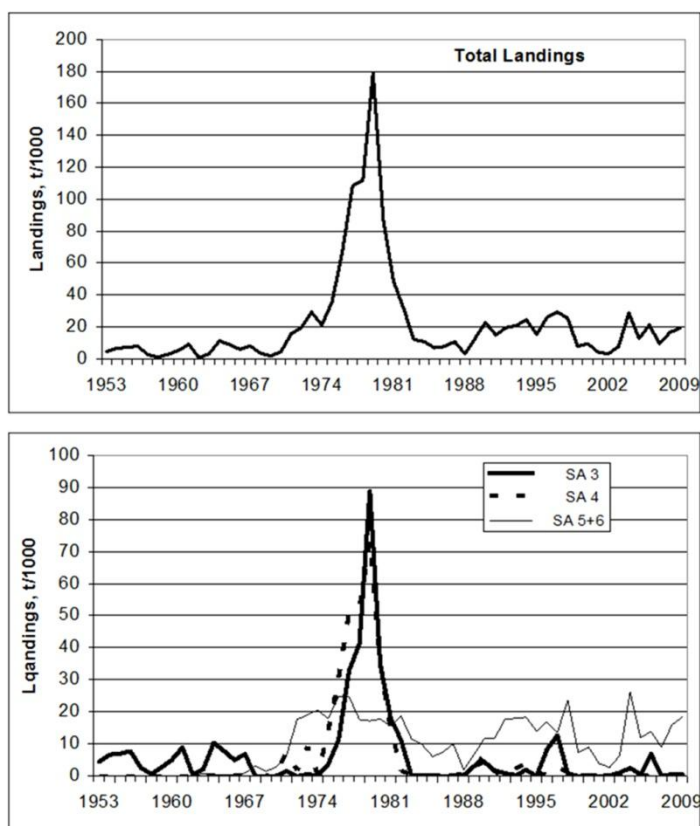


Figure 14. Recent catch statistics for *Illex illecebrosus* in total (above) and by NAFO region (below) showing the relative stability of the fishery in the southern region.

The Subarea 4 catch increased from about 400 t in 1974 to 14,000 t in 1975 and continued to increase regularly to about 73,000 t in 1979 (Figure 14). It subsequently declined regularly to about 400 t in 1983 and has remained generally low since, with a peak of about 6,500 t in 1990 and 4,000 t in 1994 (Hendrickson and Showell, 2010). Much of the Scotian shelf squid catch is taken as by-catch in the small-meshed bottom trawl fishery directed for silver hake (Waldron, 1978). Midwater trawls, also used in the directed squid fishery, catch mostly squid, the small by-catch consisting mainly of silver hake. In 1979 about 6,000 t was taken offshore in Subarea 4 by the Japanese jigging fleet (NAFO, 1980).

The northeastern USA squid fishery was also initially incidental to other (trawl and inshore trap) fisheries (Lange and Sissenwine, 1983). During 1887–1962 peak catch for *I. illecebrosus* and *L. pealei* combined was about 3,600 t in 1928. Foreign fishing began with the USSR first participating in 1964. However, during 1963–1967 the annual catch of *I. illecebrosus* remained below 1,000 t. Annual *I. illecebrosus* catch subsequently increased, though not regularly (Figure 14), due to increasing participation by foreign fleets. It increased from about 6,600 t in 1971, with five foreign fleets participating, to peak at about 25,000 t in 1976, with 11 foreign fleets participating. During that period of fishery expansion the maximum domestic catch was about 1,600 t in 1976. Annual catches generally declined to 10,000 t in 1984 and to a minimum of 2,000 t in 1988 before increasing regularly to about

18,000 t in each of 1992 and 1993. Since 1981 the USA domestic fishery has expanded and there has been no foreign participation in this fishery since 1986.

In Newfoundland the annual catch is generally taken throughout July to November, with peak catches usually occurring in September or October (Beck et al., 1994; Mercer, 1973a). Most of the catch is taken along the northeast coast of Newfoundland (NAFO Divisions 3L and 3K, Figure 13), with greatest catches usually occurring in Division 3L. In years of very low inshore squid abundance, however, local concentrations of squid may occur almost anywhere around Newfoundland.

The Subarea 4 catch is mostly taken along the edge and slope of the Nova Scotian shelf (NAFO Divisions 4VWX, Figure 13). The fishery may extend April through November. Peak catches occur earlier than at Newfoundland, with greatest offshore catches having been taken between late July and early September during 1977–79 (Amaratunga, 1981a, b). However the Subarea 4 inshore catch peaks much later. For example, in 1977 when total offshore catches and Canadian catch rate peaked in late July, the small inshore fishery peaked in September, only one month earlier than the peak catch at Newfoundland (Amaratunga et al., 1978).

Most of the short-finned squid catch in Subarea 5+6 has traditionally been taken offshore in a mixed trawl fishery that also catches *L. pealei*. Although both species are fished from the Gulf of Maine to Cape Hatteras, *L. pealei* generally has a more southerly distribution than *I. illecebrosus* (Brodziak and Hendrickson, 1999; Lange and Sissenwine, 1983). In recent years however, most of the short-finned squid catch in Subarea 5+6 has been taken from southern areas of the mid-Atlantic bight (NEFSC 1994). The *L. pealei* and short-finned squid fisheries are somewhat separated by season, with catches of *L. pealei* occurring in all months but peaking during winter in recent years. Catches of *I. illecebrosus* generally occur in all months as well, but the vast majority of the catch is taken offshore during June–September (NEFSC, 1994). Inshore catches of *L. pealei* generally peak during May–June, whereas inshore catches of *I. illecebrosus* peak during September–October (Lange and Sissenwine, 1980).

Although annual catches are strongly affected by variable fishing effort, it is believed that, for the Scotian shelf and Newfoundland, catches generally reflect annual recruitment since about 1972 (with some exceptions). Obviously, trends in catch (and recruitment) are highly variable but in synchrony at Newfoundland and on the Scotian shelf whereas the trend is for greater stability at a moderate level on the northeastern USA shelf. Relative stability in recruitment to the southern-most fishery area may be related to a relatively mild ocean climate, close proximity to the spawning ground, and recruitment from squid spawned in all seasons (Coelho and O'Dor, 1993; O'Dor and Coelho, 1993; O'Dor, 1998). In contrast, the fishery in Canadian waters depends almost exclusively on recruitment of squid spawned during winter (or in some years winter-early spring) (Coelho et al. 1994). Recruitment, especially at the most northern area (Newfoundland) is related to ocean climate (Dawe and Warren, 1993; Dawe et al., 2000, 2007). Especially evident is that uncommon prolonged periods of poor squid recruitment (1968–1974 and 1982–1993, Figure 14) are associated with unusually cold periods of ocean climate (Beck et al., 1994). One working hypothesis is that squid recruitment is limited to a moderate level on the northeastern USA shelf due to low carrying capacity (Dawe et al., 2000) that may be related to intense competition with other predators and that population increases are achieved by expansion to more northern areas when climatic conditions are favourable. Furthermore, squid abundance may co-vary with that of its most important predators, competitors and prey in an adaptive manner such that the

population increases and expands when niche space becomes available (Dawe et al., 2007; O'Dor, 1998).

4.2. Resource Management

A detailed account of the development of management regulations for each of the three fishery areas has been provided by Lange and Sissenwine (1983), O'Dor and Dawe (1998) and Dawe and Hendrickson (1998) and will be summarized and updated here. All northwest Atlantic squid resources were initially managed through ICNAF. Pre-emptive quotas, first established due to increases in catches by foreign fleets, were set at 71,000 t in 1974 (and again in 1975), for both commercially exploited squid species combined for Subareas 5+6. A separate TAC (total allowable catch) was established for short-finned squid, of 30,000 t for 1976, which was increased to 35,000 t in 1977 (Lange and Sissenwine, 1980). The Subarea 3+4 TAC was first set in 1975, at 25,000 t (ICNAF, 1975).

In 1977, both the USA and Canada extended their jurisdiction to assume responsibility for fishery resources within 200 mi of their coastlines. Since that time the USA has managed its squid resources independently. However, Canada has continued to manage its short-finned squid resource through ICNAF and NAFO.

Under the USA management system, an allowable biological catch (ABC) for short-finned squid is established annually for SA 5+6 by the Mid-Atlantic Fishery Management Council (MAFMC) (Dawe and Hendrickson, 1998). During 1978-1995, the SA 5+6 ABC was 30,000 t. It was reduced from 21,000 t in 1996 to 19,000 t in 1997 and 1998, based on the most recent stock assessment (Hendrickson et al., 1996), which concluded that the MSY was approximately 24,000 t during 1982-93, rather than 30,000 t as had been previously estimated. The TAC has since remained at 24,000 t (NAFO 2011). Commercial catch is monitored via a mandatory dealer reporting system whereby weekly purchase quantities are reported to NMFS. Under this system, the directed fishery is closed when 95% of the ABC is landed. The ABC has never been exceeded. A moratorium on the number of vessels for which short-finned squid fishing permits could be obtained went into effect in June of 1997. Since then there have been approximately 50 vessels in the directed fishery and captains are required to submit logbook reports of their fishing activities.

A minimum mesh size of 60 mm was also established for bottom trawls fishing for squid (ICNAF 1978). Information on resource status in Subarea 5+6 is based largely on indices of the abundance of pre-recruit and recruited squid from spring and autumn bottom trawl surveys. Recognizing that short-finned squid resources in USA and Canadian waters likely comprise a single population, joint management of this species across all areas is advisable. Given the annual life cycle of this species, the basis for an annual Subarea 5+6 TAC of 24,000 t should be reviewed. There may be considerable potential for recruitment overfishing in fisheries for annual species. This may be particularly true for the USA fishery area because that area may serve as a stable 'reserve' for short-finned squid in years of low total population abundance.

The TAC for Canadian waters (Subarea 3+4) was maintained at 25,000 t throughout 1975-77 but in addition, countries without specific allocations were permitted to take 3,000 t each (ICNAF, 1978). The TAC was increased from 25,000 t to 100,000 t during 1978 (ICNAF, 1978). In that year the TAC was first partitioned between Subarea 3 (45,000 t) and

Subarea 4 (55,000 t). It was further increased to 120,000 t in 1979. The 1979 TAC was exceeded by about 42,000 t and the TAC was established in 1980 at 150,000 t (NAFO, 1980). That TAC level remained in place until it was reduced to 75,000 t in 1999 and to 34,000 t in 2000. The 2000 level of 34,000 t was determined (Rivard et al., 1998) by calculating the relative fishing mortality (relative F) for the year of peak Subarea 3+4 landings (1979), by dividing the landings by the Subarea 4 July survey biomass index of that year. Assuming the 1979 fishing mortality rate would be appropriate to more recent years of low abundance, this relative F was then applied to the average survey biomass index for the period 1983-1997, to calculate the corresponding mean annual removal level that might be sustained under the recent period of 'low productivity' (Rivard et al., 1998). The 34,000 t TAC has remained in place since 2000 (Hendrickson and Showell, 2010; NAFO, 2011). Information on resource status in Subarea 3+4 is based largely on indices of the biomass from multiple bottom trawl surveys including an autumn survey in SA 5+6 as well as summer (July) and fall surveys in Canadian waters (SA 3+4) (Hendrickson and Showell, 2010). Annual assessments have concluded that the resource has remained in a state of 'low productivity' since 1983 (NAFO, 2011).

In 1977 a minimum codend mesh size was established of 130 mm for all bottom trawls fishing inside the slope area of the Scotian shelf, as defined by a small-mesh gear line (ICNAF, 1978). Outside the small-mesh gear line, short-finned squid may be taken in a directed fishery or as a by-catch in the silver hake fishery which utilizes small-meshed bottom trawls. In that slope area, where most of the Subarea 4 squid and silver hake fishery is directed, there is a minimum codend mesh size regulation for bottom trawls of 60 mm (NAFO, 1984).

In 1978 effort regulations were first introduced in the Subarea 4 foreign trawl fishery, recognizing that high TAC's could result in excessive exploitation in years of poor squid recruitment (ICNAF, 1978). Fishing days were allocated in 1978 based on catch rates achieved in the previous year. Thus, if squid abundance was lower in 1978 than in the previous year, the effort allocation would preclude the TAC being taken and would limit risk of over-exploitation. Effort regulation was discontinued with the virtual absence of directed trawl fisheries for squid following the early 1980's. It was found however that effort is somewhat self-regulating in that when squid recruitment declined to some marginal level (in 1982), foreign fleets did not fully utilize their allocated fishing days for squid, and directed their fishing activity towards other species (NAFO, 1983). There are no specific effort regulations for the Newfoundland inshore fishery. That fishery relies mostly upon passive gear (jigs and traps), and effort expenditure usually decreases with squid availability.

The season for foreign vessels fishing for squid in Canadian waters was established as beginning on June 15 in 1978 (ICNAF, 1978) and on July 1 for 1979 (ICNAF, 1979). Currently, the Subarea 3+4 season for foreign vessels extends from July 1-December 31, whereas the Canadian fishery (both inshore and offshore) is April 1-December 31.

4.3. Conservation Concerns

Trends in relative fishing mortality for SA 3+4 indicated that fishing mortality in Canadian waters was highest during the 1976-81 period of highest removals (Rivard et al., 1998). However, Dawe (1999) showed that when total fishery removals (including those from

USA waters) were considered it appears that overall fishing mortality was relatively low during the 1976-1981 period of peak catch when most of the catch was derived from SA 3+4. Highest fishing mortality occurred in 1973, when 66% of the total catch was derived from SA 5+6 (Dawe and Hendrickson 1998). It was noted that the main peak of fishing mortality in 1973 was soon followed by a regular increase in catches during 1975-1979, which corresponded to a warm oceanographic regime (Dawe et al., 2000). In contrast, a secondary peak in relative fishing mortality during 1982-1983 coincided with the onset of a prolonged period of low biomass and a cold oceanographic regime. While low total biomass from 1983 to the mid-1990s has been related to a cold thermal regime (Dawe et al., 2000, 2007), abundance has generally since remained low, despite the persistence of a warm oceanographic regime in the Canadian Atlantic since the mid-1990's (Colbourne et al., 2009). It is possible that antropogenic effects on climate variability may have resulted in de-coupling of some of the interacting ocean climate processes that regulate abundance (Dawe et al., 2007). However, the possibility that high fishing mortality during a period of low abundance was a contributing factor cannot be dismissed. This further highlights the advisability of managing this fishery resource on a total population basis across all fishery regions.

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Chapter IV

***Illex argentinus*, Argentine Shortfin Squid**

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Abstract

Illex argentinus, a close relative of the other North Atlantic *Illex* species, concentrates on the Patagonian shelf edge and spreads over the shelf from Southern Brazil to the Falkland Islands. It supports one of the world's largest squid fisheries.

The fishery mostly exploits the winter spawning, south Patagonian stock, which is more abundant, grows to a larger body size and extends further south than the summer spawners. Spawning takes place in the northern part of the range and the eggs hatch into a typical ommastrephid rhynchoteuthon paralarva. *I. argentinus* is short-lived and semelparous living approximately one year, at the end of which the squid die after spawning. Growth is rapid and the largest individuals - females from the South Patagonian, winter spawning stock - reach a mean mantle length of 330 mm (maximum of 400 mm ML) when fully grown. Large scale migrations between the spawning grounds and the feeding grounds, and back again, over the one year life cycle are accompanied by diel vertical migrations. Immature and maturing squid occur 3 - 20 m off the bottom during the day but at night they ascend to 5 - 20 m over the shelf and to 20 - 200 m beyond the shelf break. Mature squid of the South Patagonian Stock migrate northward along the continental slope to the spawning grounds in May – July remaining close to the sea bed (500 - 900 m) at night and ascend to 200-300 m above the bottom during the day.

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The paralarvae are thought to feed using their proboscis, on body mucus enriched with microorganisms and other food particles that stick to it. Juveniles and adults are opportunistic predators feeding on fishes, crustaceans, and cephalopods including smaller conspecifics.

The diet generally reflects the plankton and nekton available. Small squid < 200 mm ML eat only crustaceans but may switch increasingly to fish as they grow. Cannibalism is a feature of the largest squids. Overall, crustaceans (euphausiids and pelagic amphipods) are the main prey, representing between 71 and 99% of the diet. Off Southern Brazil *I. argentinus* is an important prey of large pelagic and demersal fishes, toothed whales and subantarctic fur seals. On the Patagonian shelf it is an important prey of common hake providing > 50% of annual food intake and is also consumed by hoki, red cod, dogfish, and various species of penguin, albatross, some petrels and several seals and dolphins. In the vicinity of the Falkland Islands the southern Patagonian stock has few important predators because squid have grown to a relatively large size before they arrive there. *I. argentinus* is host to 21 known species of parasite, mostly the larval stages of helminths and trematodes.

The fishery is pursued by trawlers but mostly by jiggers which attract the squid with powerful lights that can be seen in visible band satellite imagery. The largest annual catch to date was 1.153 tonnes taken in 1999. There are substantial variations in recruitment and stock size driven by environmental variability.

1. Introduction

Illex argentinus (Castellanos, 1960) is closely related to the north Atlantic members of the genus *Illex* but distinguished from them by the possession of longer arms (Jereb and Roper, 2010). It is a powerful, muscular squid capable of making long migrations between spawning and feeding grounds. It is abundant in the Southwest Atlantic from southern Brazil to southern Argentina and the Falkland Islands (Haimovici et al., 1998). Greatest concentrations occur on the Patagonian Shelf edge, but its distribution extends over the shelf and individuals have also been caught off the shelf as far east as the Antarctic Polar Front to the west of South Georgia (Rodhouse, 1991; Anderson and Rodhouse, 2001).

Despite its high abundance, *I. argentinus* was described relatively recently. Angelescu et al. (1958) misidentified this species as *Ommastrephes bartramii*. However, two years later Castellanos (1960) described it as a new species *Ommastrephes argentinus*, that was then subsequently changed to *Illex argentinus*. Nesis (1987) considered all *Illex* species as a subspecies of *I. illecebrosus*, but this was not widely supported. In the most recent key to cephalopods (Jereb and Roper, 2010) *I. argentinus* is considered as a separate species.

The fishery for *I. argentinus* is one of the largest cephalopod fisheries in the world. Catches are highly variable, possibly driven by environmental variability in the spawning area. In spite of this, the fishery has persisted since its inception in the early 1980s (Csirke, 1987).

The fishing fleet is dominated by jiggers fishing with lights which are visible in US Defence Meteorological Satellite Programme imagery (Rodhouse et al., 2001; Waluda et al., 2002; 2008) (Figure 1). Trawling, which yields a generally poorer quality product, accounts for a small proportion of the total catch.

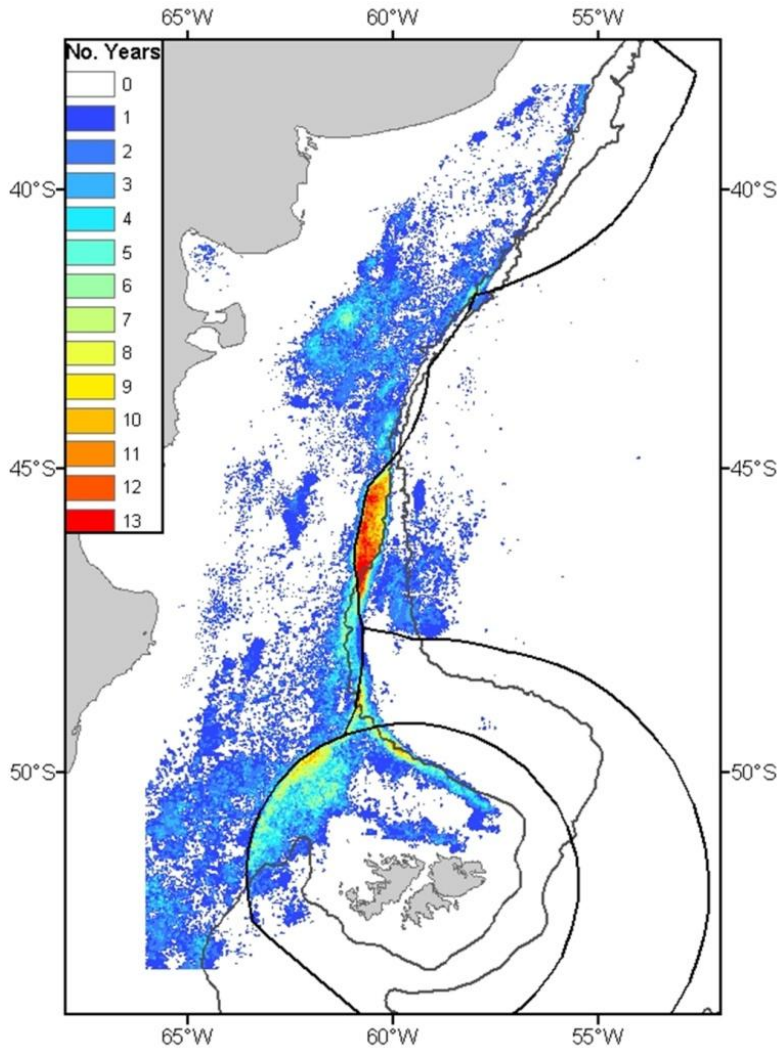


Figure 1. Distribution of fishing lights targeting *Illex argentinus* on the Patagonian shelf obtained from the Defence Meteorological Satellite Program-Operational Linescan System (DMSP-OLS) for the period 1993–2005. Legend indicates the number of years in which fishing took place in each 2.7 km grid square, with red areas indicating regions in which fishing occurred in all 13 years of the study period. Grey lines indicate 200 and 1000m depth contours. Black lines indicate territorial boundaries [High seas, Argentinean EEZ (Exclusive Economic Zone), FICZ: Falkland Islands (150 mile) Interim Conservation Zone (FICZ), Falkland Islands (200 mile) Outer Conservation Zone (FOCZ)].

2. Life History Biology

2.1. Population Structure and Life Cycle

Originally, *I. argentinus* was considered to be a single population (Sato and Hatanaka, 1983; Csirke, 1987). Then it was found that the species consisted of two populations differing both by season and place of their spawning, i.e., an abundant winter spawning population

(more than 95% of the total stock) and a small summer spawning population (Hatanaka et al., 1985; Hatanaka, 1988). Brunetti (1988) divided the winter spawning squid into two stocks, the Bonaerensis North Patagonic Stock (BNPS) and the South Patagonic Stock (SPS), differing both by feeding grounds and size of adults (medium and large, respectively). Based on the occurrence of mature females in different seasons, Nigmatullin (1989a) revealed that *I. argentinus* spawn throughout the year, and proposed subdivision of the total stock into four seasonally spawning groups adding a so-called spring spawning stock of unclear status. Although Tsygankov (1987) found qualitative differences in three loci of esterases extracted from the buccal muscles between various intrapopulation groups of *I. argentinus*, the taxonomic status of these groups remained unclear. Analysis of dynamics in length frequency compositions has shown that the life cycle of all *I. argentinus* populations is 1 year (Hatanaka et al., 1985; Hatanaka, 1986) and this was subsequently confirmed by statolith ageing investigations (Arkhipkin, 1990; Rodhouse and Hatfield, 1990).

The life cycle of the most abundant winter spawned, South Patagonian, group can be subdivided into a postparalarval period taking place in waters off Brazil and Uruguay in August and September (Leta, 1987; Santos and Haimovici, 1997); a juvenile period in shelf and oceanic waters off Uruguay and Argentina in September to December (Brunetti, 1988; Parfeniuk et al., 1992); a feeding period on the Patagonian and Falkland Islands shelves in January to April (Brunetti, 1988; Hatanaka, 1988); a pre-spawning period on the shelf edge and slope off Argentina and Uruguay in May to July (Hatanaka, 1986, 1988; Arkhipkin, 1993) and spawning in shelf and slope waters off northern Argentina, Uruguay and Brazil in July and August (Brunetti, 1988; Santos and Haimovici, 1997) (Table 1). Squid aggregate and are fished mainly during the feeding period on the shelf and the pre-spawning period on the shelf edge and slope (Nigmatullin, 1989b).

Stock structure dynamics of *I. argentinus* during the feeding period on the Patagonian shelf was studied both in the fishery region of 45-47°S outside the EEZ and within the FICZ (Falkland Islands Conservation Zone) using data obtained from Japanese jigging vessels (Rodhouse and Hatfield, 1990; Uozumi and Shiba, 1993).

It has been found that the age composition of *I. argentinus* catches changes between January and April due to gradual migrations of feeding schools. Studies of the length at age structures separately for immature, maturing and mature squid of both sexes, with a 10 day precision, gave an opportunity to reveal in detail the stock structure dynamics and migratory patterns of *I. argentinus* during the January-April feeding period on the Patagonian shelf (Arkhipkin, 2000). It has been shown that stock structure is relatively stable during the feeding period (January-April) of the winter hatched *I. argentinus*. After a massive immigration in June and July of recently hatched squid into the region 45- 47°S at the end of January to the beginning of February, from further north on the Patagonian shelf (Hatanaka, 1988; Parfeniuk et al., 1992), the age structure of squid remains reasonably stable until the middle of April. During each 10 day period, four to five month age classes have been observed. This agrees with data obtained from the jigging fishery (Uozumi and Shiba, 1993). The predominance of monthly age classes changes gradually from June-hatched squid in February to July-hatched squid in March-April.

Based on a number of biological characteristics (statolith microstructure, modal length in different months, sizes at maturity, types of feeding and pre spawning migrations), it has been concluded that the Patagonian shelf south of 45°S is a feeding ground for two intraspecific

groups of winter hatched *I. argentinus*: the “matured at medium sizes shelf group” (ShG) and the “matured at large sizes slope group” (SIG) (Arkhipkin, 1993).

These two groups correspond well with the Bonaerensis North Patagonian Stock and South Patagonian Stock (SG and OG, respectively) distinguished by Brunetti (1988) using length frequency analysis.

Table 1. Phenology of the winter-spawning South Patagonian stock of *Illex argentinus*

Spawning season	Spawning location
May – August	Slope north of 38°S in the Falkland/Brazil Current
Hatching season	Hatching location
May – August, peak in July	Probably along slope near Subtropical Front
Paralarval phase	Paralarval location
May – September	Subtropical Front and in warm >12° -14° C eddies moving southward
Juvenile phase	Juvenile location
September – October	Northern Patagonian Shelf
Young adult phase	Young adult location
November – February	Spreading across Patagonian Shelf and south towards 46° - 49° S (north of Falkland Islands)
Late adult phase	Late adult location
February – June	Patagonian Shelf around west, north and east of the Falkland Islands
Mature adults migrating towards spawning grounds	Migrating adult location
May – June	Towards the edge of the Patagonian Shelf moving northwards

The shelf group also corresponds with the winter shelf group (WSG), and the slope group corresponds well with the winter oceanic group (WOG) which were distinguished by different locations of juvenile feeding and type of life cycle (Parfeniuk et al., 1992; Nigmatullin and Laptikhovsky, 1996).

The shelf group of *I. argentinus* has a neritic type of life cycle, characterized by: 1) shelf spawning in warm waters of the northern part of the species range (27-36°S), 2) southward feeding migrations of juveniles < 100-150 mm ML over the Patagonian shelf, 3) 'shelf' type with a dark zone within the statolith microstructure (Arkhipkin, 1993), 4) fast juvenile growth but rather slow growth of immature squid, 5) medium size at maturation (males at 160-220 mm ML, 6) females of 180-240 mm ML), 7) medium maximum size of mature males of 180-260 mm ML and medium maximum size of mature females of 220-320 mm ML and 8) 'shelf' northward pre-spawning migrations. The slope group of *I. argentinus* has an oceanic/slope

type of life cycle characterized by: 1) slope spawning in the northern part of the species area (27- 36°S), 2) southward feeding migrations of juveniles < 100-150 mm ML in the open part of the Argentine Basin, 3) 'oceanic' type of dark zone within the statolith microstructure, 4) slow juvenile growth but rather fast growth of immature squid, large size at maturation (males at 180-240 mm ML, females at 240-340 mm ML), 5) large maximum sizes of mature squid (Males: 240-340 mm ML, females:280-400 mm ML) and 6) 'slope' northward pre-spawning migration. The taxonomic status of the two groups of winter spawned *I. argentinus* remains unclear (Arkhipkin and Scherbich, 1991; Parfeniuk et al., 1992; Arkhipkin, 1993; Nigmatullin and Laptikhovsky, 1996; Santos and Haimovici, 1997).

2.2. Egg Stage

Egg masses spawned by *I. argentinus* have never been observed in the wild but it can be assumed that they are very similar to those of the closely related species *I. coindetii*. These have been observed in the Mediterranean by Naef (1928) and identified by Boletzky et al. (1973). The closely related Northwest Atlantic species *I. illecebrosus* has been spawned in captivity and a single female produces an egg mass that swells to a gelatinous sphere up to 1m in diameter containing some 100,000 eggs (Durward et al., 1980). O'Dor (1983) has observed and filmed these egg masses being spawned in mid-water in tanks. When released from the mantle the egg mass is held by the arms of the female while she hovers in mid-water using fin movements. The egg mass swells rapidly and sinks when released but may later attain neutral buoyancy and float in mid-water - possibly at a pycnocline in the ocean.

Embryonic development in *I. argentinus* has been studied by Sakai et al. (1998 and 2011) who fertilized eggs artificially in the laboratory and followed their development under controlled conditions.

The technique of treating the eggs with oviducal gland jelly was developed by Ikeda et al. (1993) on *Todarodes pacificus* and subsequently used by Sakurai et al. (1995, 1996) for artificial fertilization of other ommastrephid species. In *I. argentinus* thirty developmental stages were recognised from the unfertilized egg to the hatching paralarva and these are illustrated in Figure 2a,b,c. The unfertilized eggs are oval with a long axis of around 1.02 mm and a short axis of 0.81 mm. The hatching paralarvae have a mantle length of approximately 1.6 mm.

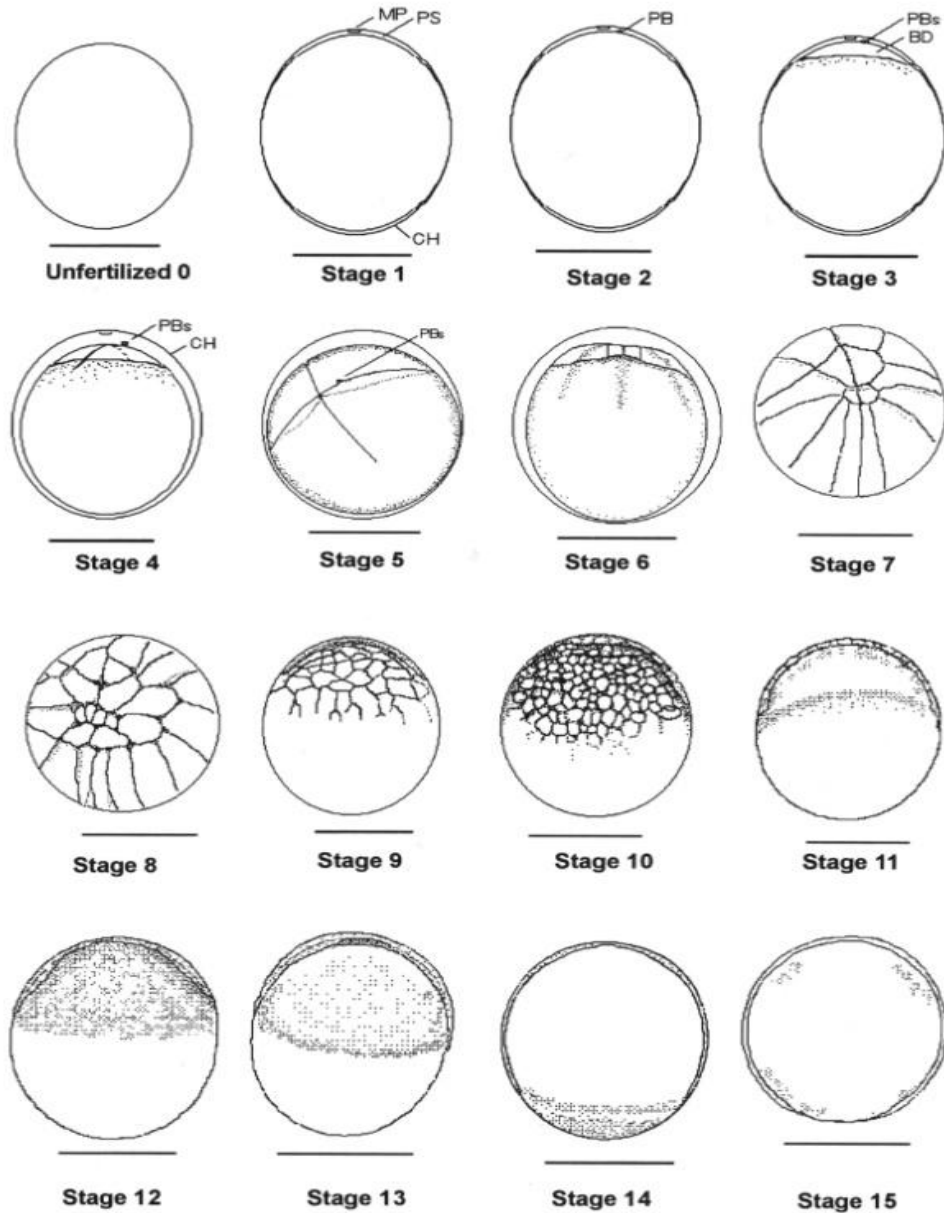
The minimum temperature for normal development is between 11.4 and 13.0°C which is broadly consistent with field observations that the paralarvae of winter spawned *I. argentinus* are not found below 14.0°C (Brunetti and Ivanovic, 1992). Embryos developed and hatched in temperatures of up to 23.2 °C, which was the maximum temperature used in experiments by Sakai et al. (1998, 2011) .

2.3. Paralarval Stage

The paralarvae of *I. argentinus* hatch as typical ommastrephid rhynchoteuthions characterised by the presence of a single proboscis in place of tentacles. Descriptions of the rhynchoteuthion stage have been provided by Leta (1987), Brunetti (1990) and Haimovici et al. (1995) and are illustrated in Figure 3. Scanning electron micrographs have also been

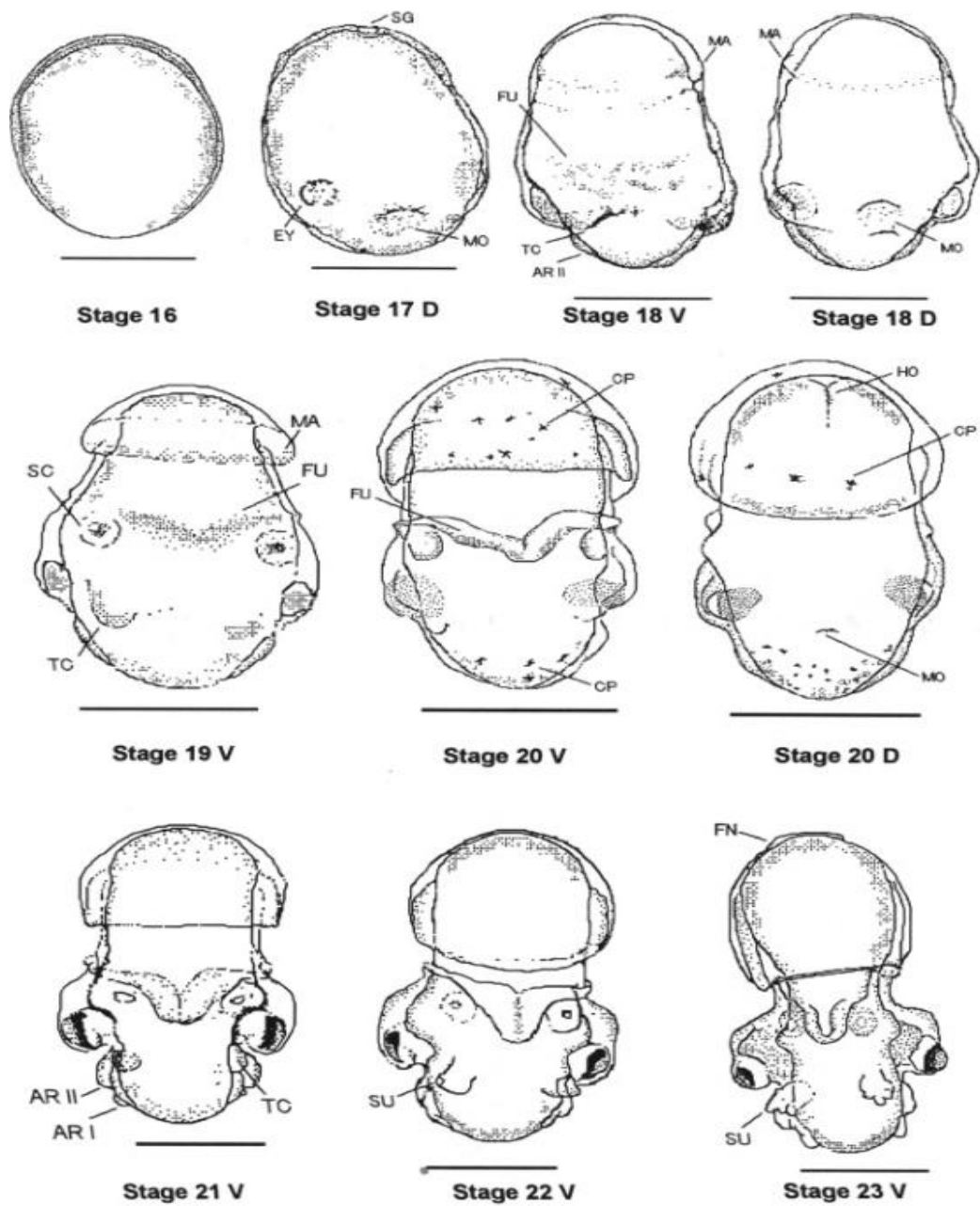
published by Rodhouse et al. (1992). With early growth the body increases in length relative to width and the mantle becomes cylindrical. Initially, the third and fourth arm pairs are vestigial, but by 6.0 mm ML they have developed and the arm formula is 2.3.1.4.

The proboscis has eight equal sized suckers at the distal end and initially it is robust but becomes relatively thin with growth. It starts to separate and form the two tentacles at 2.5 mm ML and the process is complete by 8 mm ML.



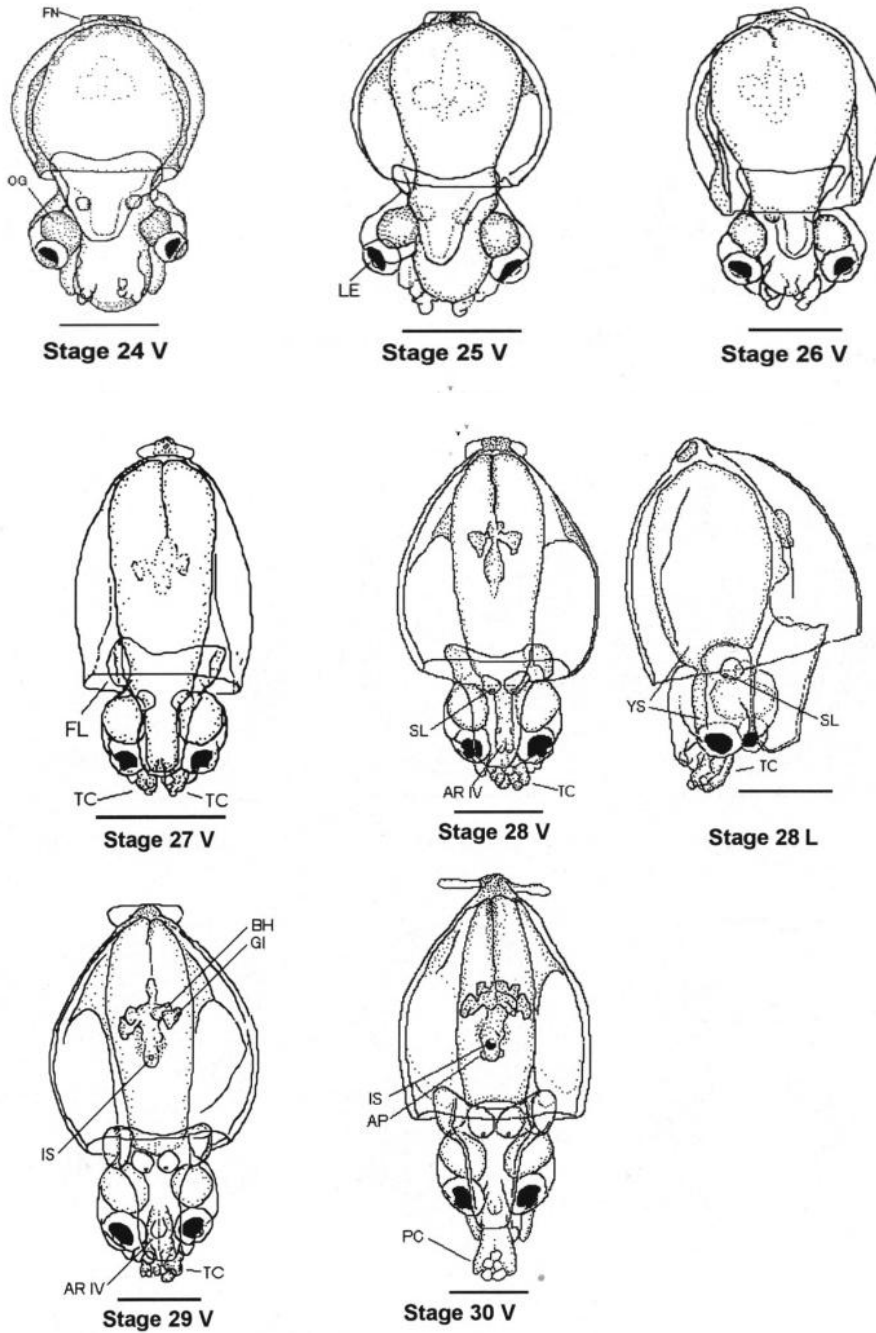
(a)

Figure 2. (Continued).



(b)

Figure 2. (Continued).



(c)

Figure 2. Developmental stages in embryogenesis, a) from stage 0 to stage 15; b) from stage 16 to stage 23 and c) from stage 24 to stage 30, of *Illex argentinus* (from Sakai et al., 1998).

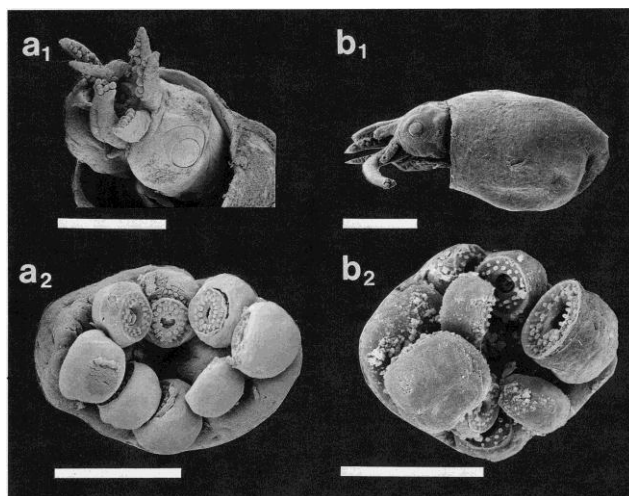


Figure 3. Rhynchoteuthoin paralarva of *Illex argentinus* (from Rodhouse et al., 1992).

The fins are small and lie at the end of the mantle at hatching but by 6.5 mm ML they are quadrangular and are positioned on the top of the mantle. There are chromatophores on the mantle and six large chromatophores on the head arranged in a petal pattern. Two large chromatophores are also present below and behind the eyes.

There are two discontinuities in the growth of paralarvae and juveniles (Vidal, 1994). The arms, tentacles and fins grow rapidly up to 14 mm ML, and separation of the proboscis into the two tentacles is not accompanied by other morphometric changes. There is then a second stage between 14-28 mm ML when the tentacles and their clubs develop rapidly. In the third stage between 28-55 mm ML the body develops a more elongated form.

2.4. Age and Growth

In common with many other temperate cephalopod species *I. argentinus* is short-lived and semelparous; having a life span of approximately one year, at the end of which the squid spawn and die. Growth is rapid and the largest individuals - females from the South Patagonian, winter spawning stock - reach a mean mantle length of 330 mm (maximum of 400 mm ML) when fully grown.

2.4.1. Ageing Methods

Fundamental to assessing growth is the ability to age individual squid. In *I. argentinus* analysis of age has focused on use of growth increments in the statolith which were first identified in the genus *Illex* by Lipinski (1978) and Hurley et al. (1979). These increments were subsequently shown to be produced daily by treating squid held in captivity with marker chemicals (strontium chloride, oxytetracycline and chlortetracycline) which enabled increments of known date to be identified in ground sections of the statoliths (Dawe et al., 1985; Hurley et al., 1985; Lipinski, 1986). Growth increments in the gladius cannot be used to age squid as they become indistinct with time but the spacing of more recent increments reflects daily growth in ML and they have been used to reconstruct growth in mantle length in

squid that have been aged by reading statolith growth increments (Arkhipkin and Perez, 1998).

2.4.2. Growth Data from Statoliths

Paralarval statolith growth has been observed in newly hatched *I. argentinus* up to 10 days old using alizarine staining (Sakai et al., 2004). The maximum statolith radius (MSR) of newly hatched paralarvae is some 21.1 μm and daily growth of MSR ranges from 3 -7 $\mu\text{m day}^{-1}$, depending on rearing temperature. The natal ring forms at 21 μm MSR.

Growth determined from growth increments in *I. argentinus* statoliths has been estimated by Arkhipkin (1990), Rodhouse and Hatfield (1990), Arkhipkin and Scherbich (1991), Arkhipkin (1993), Uozumi and Shiba (1993) and Arkhipkin and Laptikhovsky (1994). These studies confirmed earlier work on analysis of modal ML progression by Hatanaka (1986) who concluded that life span was about 1 year.

The form of the growth curve of *I. argentinus* and other squid species, based on statolith data, has been a subject of much discussion among cephalopod workers. For *I. argentinus* the following growth models have been fitted to data: von Bertalanffy (Hatanaka, 1986; Brunetti and Ivanovic 1990), linear (Koronkiewicz, 1986; Arkhipkin, 1990; Rodhouse and Hatfield, 1990; Arkhipkin and Scherbich, 1991), power and exponential (Schwarz and Perez, 2010), and Gompertz and Schnute (Uozumi and Shiba, 1993; Arkhipkin and Roa-Ureta, 2005; Schwarz and Perez, 2010). In most cases data were limited to the restricted range of size and age of squid taken by the commercial fishery. This problem was overcome by both Arkhipkin and Roa-Ureta (2005) and Schwarz and Perez (2010) who collected squid over most of their ontogeny. In all cases migration is liable to cause bias in growth estimates (Hatfield and Rodhouse, 1994).

There is evidence that squid growth is divided into stanzas with more or less sharp demarcations between each stanza (Forsythe and Van Heukelem, 1987; Arkhipkin and Roa-Ureta, 2005) and this pattern has been explained in terms of physiological energetics by Grist and Jackson (2004). The good fit of Gompertz and Schnute models in Uozumi and Shiba (1993), Arkhipkin and Roa-Ureta (2005) and Schwarz and Perez (2010) studies of *I. argentinus* is consistent with two distinct growth phases with the discontinuity following the early-life phase marked by the inflection in the modeled growth curves.

There are several general conclusions that can be drawn:

- 1) There is considerable variation in the age that the squid reach sexual maturation both within and between seasonal cohorts. From the data pooled over years for each hatching month of winter-spawning squid, mean age at the beginning of maturation decreased with month of hatching. August and September-hatched males started maturing at 10-15 days younger than males hatched in June and a month younger than males hatched in May. Early-maturing males usually mature at age 220-250 days, late-maturing males at age 260-310 days. Thus, maturation requires about 1.5-2 months in the early-maturing males and 2-2.5 months in late-maturing males (Arkhipkin and Laptikhovsky, 1994).
- 2) Growth rates of immature squid of both sexes are similar but once sexual maturation commences females grow faster and attain a larger size than males. An effect of sex on growth in mantle length was observed in *I. argentinus* at age > 180 days when the

instantaneous relative growth rate of females became greater than that of males. At age 270-300 days, female mantle length (ML) for any hatching-month was 30-50 mm greater than that of males. At age 180- 240 days, males were heavier (despite being shorter) than females; at age 240 days, the body weight (BW) of males and females became similar and at age > 240 days females were heavier than males (Arkhipkin and Laptikhovsky, 1994).

- 3) Winter spawned squid hatched late in the season tend to grow faster than those hatched earlier, as hypothesized by Forsythe (1993) on the basis of laboratory experiments. For example, differences in size-at-age and growth rates of different hatching-months within one year were shown for squid hatched in winter 1987 and captured during the fishery in 1988. Within the age range studied (150-360 days) and at any age, the May-hatched squid were the smallest in both ML and BW. The ML and BW, at any age increased with month of hatching from May to September. All hatching-months differed significantly from each other. The minimum difference due to month of hatching in length-at-age and weight-at-age for both sexes were observed between the May and June- hatched squid, the maximum between the May and September-hatched squid. In contrast, the instantaneous rates of growth (G , % d^{-1}) of ML and BW showed a reverse pattern in squid at age > 180 days: the May-hatched squid usually had the highest G and the September-hatched squid the lowest G . However, due to considerable differences in sizes between those two hatching-months at age 180- 210 days, the relatively small May-hatched squid did not attain the sizes of large September-hatched squid, despite the fact that they had higher relative growth rates (Arkhipkin and Laptikhovsky, 1994).

Few data on squid growth, including for *I. argentinus*, indicate any strong tendency for growth to asymptote but it has been argued that the von Bertalanffy function is applicable to squid (Pauly, 1998) and similar arguments could be made for Gompertz and Schnute functions. The absence of a tendency to an asymptotic growth phase can be explained if the squid die after spawning before, or soon after reaching the asymptotic phase. This argument leads to the suggestion that squid display evidence of progenesis - at least in terms of their physiological energetics (Rodhouse, 1998). They have evolved to be semelparous and over their relatively short life span their life-time energy budget seems to resemble that of the first year of growth of longer lived iteroparous molluscs. So, in common with young iteroparous molluscs, with long life expectancy, they exhibit little or no tendency to asymptotic growth.

2.4.3. Data from Gladius Growth Increments

Growth of individual *I. argentinus* based on reconstructions of changes in mantle length over time, from gladius increments, has been described by Schroeder and Perez (2010) who showed that there are growth rate differences related to the season in which squid were spawned and to whether they were spawning on the shelf break or slope. Winter and spring spawned squid and those that spawn on the slope had the highest growth rates. High growth in the winter spawned squid occurs apparently because this group migrates to the cool but biologically productive waters of the southern Patagonian Shelf where they grow fast and reach a relatively large size before they make the spawning migration back to warmer, but less productive, waters off southern Brazil.

2.4.4. Allometric Growth

Aspects of allometric growth of the paralarval phase of *I. argentinus* are described in section 2.3 above. There are several trends in allometric growth in adult *I. argentinus* which are mostly related to the shift of resources with age from somatic to gonadal growth (Rodhouse and Hatfield, 1990, 1992) and sexual dimorphism related to maturation. Adult males have much larger and wider heads and longer arms than females of the same mantle length (Roper and Mangold, 1998).

The digestive gland in both sexes grows relatively faster than other somatic tissues, is rich in lipid in both males and females and has the highest energy content of all organs. As a percentage of body mass it increases from a mean of 6.1% in immature and early maturing squids to a mean of 10% at stage IV. It then gradually decreases to a mean of 7.8% in advanced prespawners at stage V in early June. In males it is 3.3 – 5.2% in immature and maturing squid (stages II – IV) and peaks at a mean of 8.5% in mature squid sampled in May (de Moreno et al. 1998). During the last 50 days of foraging on the southern Patagonian shelf most energy intake is directed to the digestive gland (40% in males; 47% in females) and other somatic growth (54% in males; 38% in females) (Clarke et al., 1994).

Illex argentinus maintains high feeding rates and conversion efficiencies in relation to body size and a relatively high metabolic rate until it reaches maturity. Feeding rates in *I. argentinus* (4.3-4.8% total body kilojoules day⁻¹) are similar to those in other squid (Clarke et al., 1994). However, the gross growth efficiencies calculated for *Illex argentinus* (17-22%) are generally lower than reported for some other cephalopods (27-69%) (O'Dor and Wells, 1987).

To enable rapid growth, the digestive gland must maintain relatively high absorptive capacity throughout life by increasing its relative mass. This is because of the way absorptive surface scales on mass. The capacity for storage by the digestive gland also increases with squid size. As the squid are feeding and growing energy requirements are met from the food, but once they start the spawning migration, energy stored in the digestive gland is probably utilised to partially fuel the energetic cost of swimming. Positive allometry of the reproductive organs is to be expected in these squid, which grow fast and spawn once towards the end of their life. Energy and nutrients are diverted to somatic growth in young squid and shifted towards gonadic growth in later life. There is wide variation in the body size at which full sexual maturity is attained in *I. argentinus*. In females both ovary mass and nidamental gland mass increase with maturity independently of body mass (Hatfield et al., 1992).

2.5. Maturation and Fecundity

The reproductive biology of *I. argentinus* is generally similar to that of other ommastrephid squid. Males mature earlier and at a smaller size than females. Bi-flagellate spermatozoa are packed into spermatophores that are accumulated in the Needham's sac prior to promiscuous mating.

However, in contrast to all other ommastrephids, at copulation the spermatophores are attached inside the mantle cavity because all squid of the genus *Illex* lack special female organs of sperm storage.

2.5.1. Female Reproductive System and Female Fecundity

Females possess a single ovary, two nidamental glands and paired oviducts each bearing an oviducal gland at its distal end (Figure 4). These glands provide the coating for the eggs which absorb water and expand the egg mass once it is released. The juvenile ovary has a central core of muscular connective tissue, a cortical zone where the protogonia are located and a thin epithelium where ovarian follicle cells originate. Oogenesis is asynchronous and follows the same pattern as in other ommastrephid squid. Initially oocytes are round with a nucleus situated in the centre and occupying most of the cell volume. During early stages of growth (protoplasmic growth) the nucleus slightly shifts to the future animal pole, and follicular cells appear attached to the vegetative pole at an oocyte size of ~ 0.3 mm. Afterwards they multiply and spread around the egg forming the follicular envelope (a simple follicle). This process is complete at an oocyte size of ~ 0.4 mm. Follicular cells then change their shape from flat to cuboid and form folds that gradually penetrate deep into the egg increasing its length to 0.5 mm. At this size they start to secrete yolk and the oocyte quickly grows to its final size of 1.2-1.3 mm along the major axis - including the follicular sheath (Laptikhovsky and Nigmatullin, 1992).



Figure 4. Female reproductive system of *Illex argentinus*.

Oocyte development is accompanied by growth of the entire reproductive system. The ovary of mature squid is some 5.0 to 6.2% BW, oviducts together with oviducal glands between 8 to 11.6% BW, nidamental glands between 6.0 and 7.6% BW, the entire reproductive system being between 20 and 25% BW (Laptikhovsky and Nigmatullin, 1992). The high energy demand for this growth is met by intensive feeding which also enables sequestration of energy reserves in the digestive gland to power future migration (Clarke et al. 1994; Hatfield et al., 1992).

Ovulated eggs are slightly smaller than the largest oocytes in the ovary because of the loss of the follicular envelopes. They are 0.75 - 1.2 mm (0.34-0.50 mg) and their size increases with female mantle length (Laptikhovsky and Nigmatullin, 1993). They are gradually accumulated in oviducts prior to being released at spawning. Female potential fecundity (PF) increases with squid size from 75,000-100,000 (ML 170-180 mm) to 800,000-1,200,000 (ML 350-380 mm) according to the following equations:

$$PF = \exp(2.292 + 0.162 \text{ ML}), r=0.80$$

$$PF = \exp(4.336 + 0.00604 \text{ BW}), r=0.86$$

The number of yolk oocytes (both ovary and oviduct combined) is much lower at between 17,000 and 300,000 (Rodhouse and Hatfield, 1990; Laptikhovsky and Nigmatullin, 1993; Santos and Haimovici, 1997), which is probably about a half of actual fecundity.

Actual fecundity is some 60-70% of the PF and is spawned in several egg masses, the rest being subject to atresia (Laptikhovsky and Nigmatullin, 1993). The number of oocytes in maximally full oviducts, which is a proxy for egg mass size, varies from 20,000-30,000 (ML ~170 mm) to ~200,000 (ML 320-350 mm). Such full oviducts are only observed in pre-spawning females.

It is assumed the number of eggs is reduced in each egg mass produced as the female gradually becomes exhausted. This is accompanied by shrinking of the digestive gland, as the energy store it contains is used for further egg production, followed by degeneration of the mantle which becomes thin in the final phase of the spawning process (Laptikhovsky and Nigmatullin, 1993). This spawning pattern is observed in the Summer Spawning Stock that does not undertake significant pre-spawning migrations. Squid of the South Patagonian Winter Spawning Stock have to rely on energy stores in the digestive gland for long distance migrations to spawning grounds and might be restricted in their potential to produce more than one egg mass.

2.5.2. Male Reproductive System and Fecundity

The male reproductive system consists of a single median testis with seminiferous tubules where the spermatocytes develop into mature spermatozoa (Figure 5). These become encapsulated in spermatophores which are held in the Needham's sac (spermatophoric sac) until mating. In juveniles the seminiferous tubules are not developed and only spermatogonia are present.

In subadults, the tubules are clearly developed and are some 220 µm high and there are many primary spermatocytes, some secondary spermatocytes and spermatids. In mature males the tubules are 330 µm high and there are many spermatids and spermatozoa. Spermatozoa follow the spermaduct into the so-called spermatophoric complex of organs (SCO, Figure 6).

There they are "weaved" into a seminal reservoir and while passing through the different sections of the SCO become covered by layers of specialised tunics to form spermatophores which are eventually stored in the Needham's sac prior to copulation. The SCO begins to function in maturing males before sperm enters the spermaduct. The first, tentative spermatophore production is aberrant and does not contain sperm. Normally it is not retained in the Needham's sac but is expelled from it. A few of the first, normal spermatophores with small sperm reservoirs are also expelled: neither they nor the anomalous first spermatophores

have been found in mature pre-copulatory males, but only in maturing squid (Laptikhovsky and Nigmatullin, 1992).

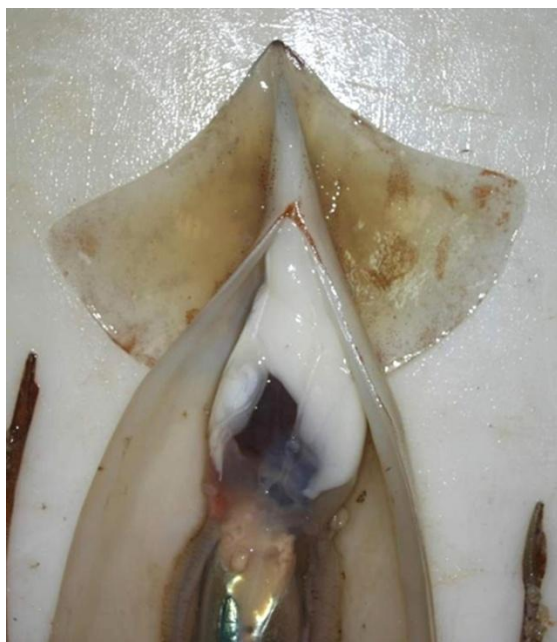


Figure 5. Male reproductive system of *Illex argentine*.

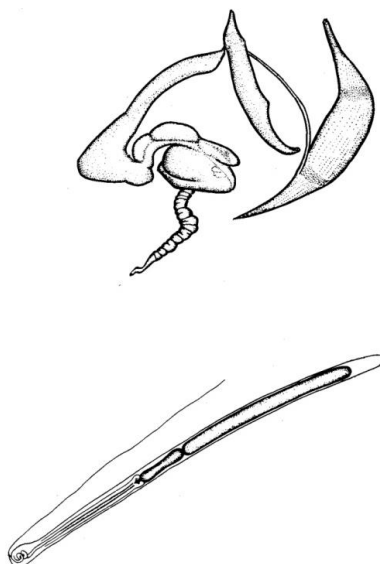


Figure 6. Spermatophoric complex of organs (SCO) and normal spermatophore of *Illex argentine*.

The number of spermatophores in mature males with a full Needham's sac varies with animal size from ~150 (170 mm ML) to ~1,400 (310 mm ML). Smaller males produce smaller spermatophores; 9 mm - 34 mm respectively. Spermatophore size also increases within each individual squid because the SCO grows together with the body so younger

spermatophores are always larger than the older ones that are situated closer to the “penis” (Laptikhovsky and Nigmatullin, 1992).

Spermatozoa of the genus *Illex*, including *I. argentinus*, are unique among the oegopsids in possessing two functional tails. Spermatozoan head length is $\sim 5.5 \mu\text{m}$ and flagella $\sim 50 \mu\text{m}$. The mitochondrial part is spur-like as in other squid. The velocity of spermatozoa in sea water is 130-140 $\mu\text{m/s}$, which is close to the maximum values registered among animals. Each spermatophore contains 17-79 million spermatozoa (Laptikhovsky and Nigmatullin, 1996).

Mature males of the South Patagonian Stock (250-270 mm ML, 450-600 g BW) usually have 1,200-1,400 spermatophores prior to starting their migration to the spawning grounds. The stock of sperm in the spermaduct (7.4-19.3 billions) is sufficient to produce an additional 200 to 300 spermatophores (Laptikhovsky and Nigmatullin, 1996). This would require another 10 to 20 days taking into account spermatophore production rate at around 15 to 20 per day (Arkhipkin and Laptikhovsky, 1994). Total spermatozoa production by a single male is estimated to be 50-100 billion (100-200 million per 1 g BW or $\sim 100,000$ per egg). In fully mature males the weight of the reproductive system is ~ 6 -9% BW, and testis weight alone is 2.9-6.3% BW (Laptikhovsky and Nigmatullin, 1992).

During spawning the testis quickly degenerates and virtually disappears, and the spermaduct becomes progressively thinner. The last spermatophores produced have short seminal reservoirs that also become semi-transparent because of the low sperm content.

2.5.3. Copulation and Spermatophore Transfer

As in other ommastrephids, spermatophores are transferred to females by a hectocotyliised arm. In *I. argentinus* it is either the fourth left arm (50.2% in a sample of 2,306 mature males) or the fourth right arm (49.8%). Copulation occurs in a “head-to-head” position, and depending on which arm is hectocotyliised, spermatophores might be deposited either on the left or right hand side, on the gill and around the oviducal glands. Upon ejaculation spermatophores are self-attached to the body as spermatangia. Attachment of numerous spermatangia to the gills is frequent and does not impact on female viability.

Because copulation is promiscuous, females of the Summer Spawning Stock carry 1-13 bunches of spermatophores with 10-150 spermatangia in each bunch. The maximum number of spermatangia was found to be 728, but normally this does not exceed 200-300, which is approximately the total male fecundity in this stock of small-sized animals. Spermatangia length differs between bunches in spent females indicating separate copulations, which probably take place prior to each egg mass being released (Laptikhovsky and Nigmatullin, 1992).

2.6. Biochemical Composition and Energetics

For many marine invertebrates, reproduction and the period leading up to it is the most energy intensive part of their life, and Darwinian fitness is optimised by balancing the demands of activity, growth and reproduction. In many organisms the energy needed for gonad production is provided by a combination of increased feeding activity and the utilization of stored energy reserves. In semelparous species body tissues may also be

exhausted to maximise gonad production. This happens in *Octopus vulgaris* in which mantle protein is depleted to increase the energy available for egg production (O'Dor and Wells 1978; O'Dor et al., 1984). However, in squid such as *Illex*, which are also semelparous, there is a need to remain in the water column and migrate to the spawning grounds in the period immediately leading up to spawning so there must be a different strategy. Ommastrephid squid, including *Illex coindetii* and *Todaropsis eblanae*, take energy for egg production directly from food, rather than from reserves (Rosa et al., 2005).

In most somatic tissues in *I. argentinus* from the South Patagonian winter spawning stock the proximate biochemical composition does not vary with sexual maturation but the mass of somatic and gonad tissue increases substantially (Clarke et al., 1994). In females the composition of the ovary, as well as the nidamental glands and oviducal glands, changes significantly with maturation. The ovary accumulates large amounts of protein and lipid and the nidamental gland accumulates mainly protein and carbohydrate and an unknown component that may be of low molecular weight such as an amino sugar or polysaccharide derivative. In males the major component of the mature testis is protein (~50% dry weight, DW) with smaller amounts of lipid and carbohydrate. About 30% of the DW has a nitrogen content which is consistent with it being DNA. In the spermatophoric complex an unknown fraction of the biochemical composition may be an amino acid or a short polypeptide. The digestive gland is rich in lipid and it accumulates substantial energy reserves whilst the squid are reaching sexual maturity on the feeding grounds of the southern Patagonian Shelf. There is no evidence that the digestive gland or the mantle tissue becomes depleted to supply energy or nutrients for gonad maturation at this time, before migration. On the feeding grounds, energy demand for tissue synthesis by females during sexual maturation is about twice that of the smaller males. Total energy demand for reproductive tissues is about 5% in males and 15% in females. Most energy consumed on the feeding grounds is directed towards growth of the digestive gland and other somatic growth. In the lead up to the northwards spawning migration energy intake is 4-5% of body energy content per day and growth efficiency is low at 17 - 22%. In the absence of feeding during the spawning migration the energy reserves in the digestive gland at the end of their time on the feeding grounds could fuel migration for 21 days in females and 14 days in males. Calculations by Clarke et al (1994) suggest that this is insufficient for them to reach the spawning grounds without feeding en route.

3. Ecology

3.1. Distribution and Abundance

Illex argentinus is distributed over the continental shelf and slope of the Southwest Atlantic from the approximate latitude of Rio de Janeiro (22°S) to Burdwood bank (55°S) including the Falkland Islands, Islas de los Estados and Tierra del Fuego (Haimovici et al., 1998; Figure 7).

It occurs at depths of between 80 and 1200 m at bottom temperatures from 2.1 to 17°C (Korotkov et al., 2006; Roper et al., 2010). The zone of maximum abundance is between 40°S and 52°S.

Paralarvae and early juveniles occur in warm water with surface temperatures 12-20°C. Hatchlings of the Bonaerensis – North Patagonian stock (BNPS) and the South Patagonian Stock (SPS) are found mostly to the north and at the Subtropical Convergence between 29°S and 36°S, particularly in offshore frontal waters of the Brazil Current. Those of the Summer Spawning stock (SSS), which reproduce in the warmest season, might occur on the shelf as far south as at 46°S (Brunetti, 1990; Haimovici et al., 1998; Waluda et al., 2001a).

The adults are concentrated in shelf and slope waters of Subantarctic origin (8° to 12°C), mainly occupying the cold frontal waters of the Falkland Current. Large squid of commercial size are present in catches all year round but are most abundant in late summer to winter and are derived from the winter peak of spawning.

3.2. Migration/Horizontal Movements

There are several stocks with overlapping ranges and different migratory patterns. Relations between those stock units are not always entirely clear and the level of genetic isolation between them has not been determined. Generally the following three types of ontogenetic/seasonal horizontal migration are found among the stocks.

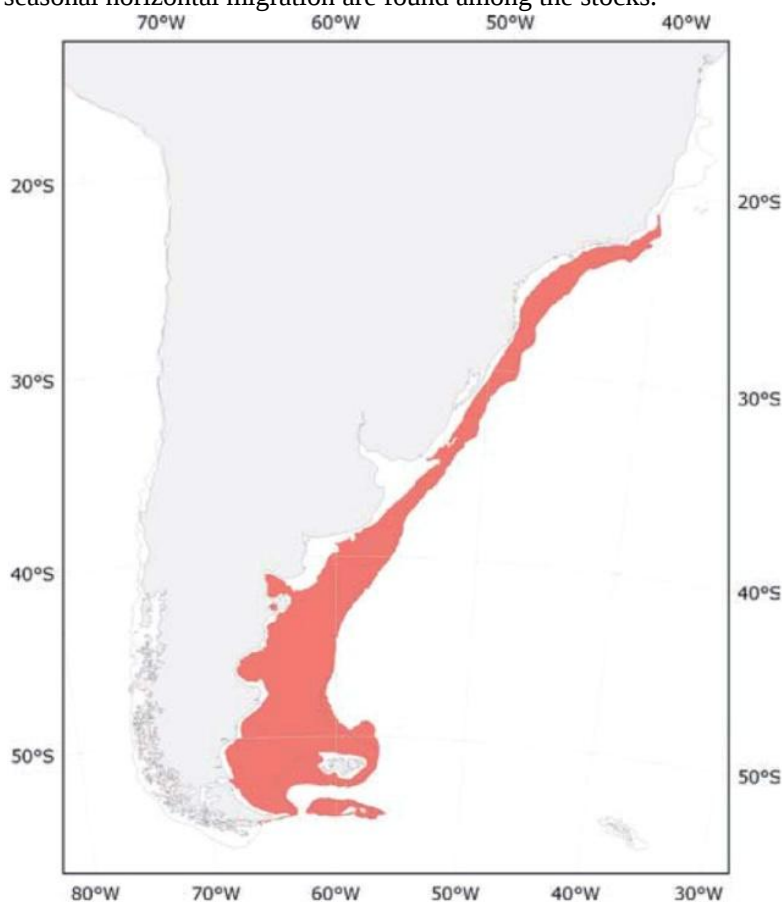


Figure 7. Distribution of *Illex argentinus* in the Southwest Atlantic. (from Jereb and Roper, 2010).

3.2.1. Inshore Migrations

Some squid make minor horizontal migrations restricted to the outer shelf. These minor horizontal migrations are characteristic of the SSS and SpSS (Spring Spawning stock). The complete life cycle of the squid in these populations occurs between 41°S and 48°S and within a depth range 50-200 m (Haimovici et al., 1998; Crespi et al., 2008).

3.2.2. Inshore-Offshore Migrations

These migrations are characteristic of the BNPS which is distributed between 26 and 48°S. Mature squid occur and spawn (mostly in winter, July–August) in upper slope waters along the western boundary of the Brazil-Falkland confluence zone and that of the Brazil Current itself. Reproduction takes place from 26°S to 38°S, at 360-520 m, down to a maximum of ~700 m (Haimovici et al., 1998; Perez et al., 2009). After a short period of initial growth in surface slope waters, juveniles migrate onto the shelf to forage. Whilst foraging they gradually move south along the Patagonian shelf as far as 49°S and once mature they return northeast to the spawning grounds. This migration occurs along the upper slope, where they aggregate along the 300-400 m contour. Similar ontogenetic behaviour is found in the South Brazil Stock (SBS) whose spawning grounds are situated at depths < 360 m (Haimovici et al., 1998; Perez et al., 2009).

3.2.3. Large-Scale Shelf-Slope Migrations

These are confined to the South Patagonian Winter Spawning Stock (SPS). Juveniles forage in oceanic waters between 35°S and 47°S (Parfeniuk et al., 1992). After reaching some 100 mm ML they migrate to the colder waters of the southern Patagonian shelf, where they forage between 40 and 49°S. As sea temperature rises immature squid migrate southward reaching about 53°S in December and January. In February and March they move closer to the shelf edge north of 52°S. In late April to June, once mature, the squid descend to depths of 600-700 m and begin the northbound spawning migration at speeds of approximately 23 km day⁻¹ between 52°S and 46°S and approximately 29 km day⁻¹ between 46 °S and 42 ° S (Arkhipkin, 1993). Females, being larger are able to swim faster. Males are the first to start migrating, some two to three weeks earlier than females, so they arrive at the spawning grounds simultaneously with females (Arkhipkin, 1993). Following the start of the male migration the sex ratio over the foraging grounds in late autumn gradually changes to a predominance of females. Migratory schools starting from ~300 m at the latitude 49°S cross latitude 46°S at ~600 m, and at latitude 42°S they are at 600-800 m, so they possibly descend even deeper further north. Squid of the SPS spawn mostly in June to August somewhere north of latitude 38°S but probably at a much greater depth than the BNS. It has been suggested that spawning occurs between 45°S and 48°S (Haimovici et al., 1998; Nigmatullin, 1989). However, this seems unlikely for the following reasons. No paralarvae have ever been caught in oceanic waters south of 40°S. Temperatures (even at the surface) are too low for successful egg development, which in *I. argentinus* takes place at 11.4 - 13°C (Sakai et al., 1998; 2011), so this is the likely minimum at which *I. argentinus* paralarvae could normally be expected to be found. It is also clear that squid schools in deep water at 42°S are dominated by females in June/July revealing that they are still migrating and not yet reproducing.

3.2.4. Vertical Migrations

Illex argentinus have two contrasting patterns of vertical migration depending on their biological condition and distribution. Immature and maturing squid foraging on the shelf and uppermost slope are found at depths of between 3 to 20 m off the bottom during the day. At night they ascend to the upper water layers (usually between 5 and 20 m, though sometimes only to 50 m) on the shelf and between 20 and 200 m beyond the shelf break.

Mature squid of the South Patagonian Stock that migrate northward along the continental slope to the spawning grounds in May – July behave differently. They remain close to the sea bed (500-900 m) at night and ascend to 200-300 m above the bottom during the day. Presumably this enables them to overlap with, and forage on, pelagic plankton and mesonekton which is migrating downwards during daylight hours (Korotkov et al., 2006; Nigmatullin, 1989).

3.3. Feeding Ecology and Behaviour

Paralarval *I. argentinus* (as in other ommastrephids) are thought to feed on body mucus (enriched with microorganisms and other food particles that stick to it) using their proboscis. Mucus has been found in their stomachs together with dinoflagellates, ciliates, bacteria and the remnants of copepods (Vidal and Haimovici, 1998, 1999).

Juveniles and adults are omnivorous, opportunistic predators that feed on fishes, crustaceans, and cephalopods of suitable size, including smaller conspecifics (Ivanovic and Brunetti, 1994). The feeding spectra in different parts of the species range reflect the plankton and nekton composition, diversity, and abundance. Squid < 200 mm ML eat only crustaceans. In larger specimens fish appear in the diet and the proportion increases with growth. Cannibalism is confined to the largest squid (Santos and Haimovici, 1997). Overall, crustaceans (euphausiids and pelagic amphipods) are the main prey of the species, representing between 71 and 99% of its diet (Ivanovic, 2010).

Illex argentinus forages in a very patchy environment. From Brazil to the Falkland Islands an individual usually encounters and feeds on only one prey type at a time, and some 55-80% of stomachs with food contain only a single prey species (Santos and Haimovici, 1997; Mouat et al., 2001; Ivanovic, 2010).

Underwater observations have revealed that *I. argentinus* hunt in small schools of between 5 and 150 individual squid, usually of similar sized animals. Within the school, squid move in different directions attacking fish and euphausiids. They show more interest in jigs when they are being drawn up through the water column rather than on their way down which probably demonstrates a general preference for upwards movement of prey. An attack on a prey item by one squid in a school provokes hunting behaviour in others resulting in a mass “feeding frenzy” (Korotkov et al., 2006).

At dawn (06:00 – 07:00) about 60-75% of squid have empty stomachs (Ivanovic, 2010; Laptikhovsky, 2002; Mouat et al., 2001). They forage actively in daylight and by early afternoon most (75-100%) have some food in their stomachs. Feeding continues during the afternoon and stomach fullness increases (Ivanovic, 2010). Around sunset and shortly afterhunting activity is low possibly because their planktonic prey disperses as it makes its upwards diurnal migration at this time. At dusk the squid migrate upwards themselves digesting food consumed in daylight. Stomachs gradually emptied by ~ 22:00, and around

that time there is a first peak of night feeding and catchability on fishing jigs. After some slowing down between 23:00 and 03:00 when the percentage of empty stomachs increases (Koronkiewicz, 1986), the second peak of night feeding and vulnerability to jigs takes place between 03:00 and 05:00 and this extends into the twilight hours of morning (Laptikhovsky, 2002). This daily feeding pattern is consistent across the entire Patagonian shelf between 43°S and 55°S. Off South Brazil foraging is mostly at dusk and in the early night (Santos and Haimovici, 1997).

Foraging activity patterns are essentially the same between sexes and different maturity stages when squid are foraging together (Ivanovic and Brunetti, 1994; Santos and Haimovici, 1997; Ivanovic, 2010).

3.3.1. Regional Variations in Diet

The main prey off Southern Brazil is fish, including the hake, *Merluccius hubbsi* and some slope-oceanic fish species including myctophids, grenadiers and pearlsides *Maurollicus muelleri*. Cephalopods are second in importance and conspecifics are the most frequently consumed (67%). Crustaceans are represented by copepods, euphausiids, mysids and decapods (Santos and Haimovici, 1997; Haimovici et al., 1998).

The hyperiid amphipod, *Themisto gaudichaudi*, is the principal squid food on the North Patagonian (34–40°S), the South Patagonian (43–55°S west of 61°W) and the Falkland Islands (49–52°S, east of 61°W) shelf areas representing >50% of the total food consumption. The second principal prey are euphausiids, particularly *E. vallentini* and *E. lucens* (Ivanovic and Brunetti, 1994; Mouat et al., 2001; Laptikhovsky, 2002; Ivanovic, 2010;).

Of the fish prey, on the north Patagonian Shelf, the main species taken are myctophids (*Gymnoscopelus*, *Protomyctophus*, *Lampichthys* spp.), anchovy (*Engraulis anchoita*) and to a minor extent Sciaenidae (Ivanovic and Brunetti, 1994; Haimovici et al., 1998). On the southern Patagonian Shelf squid consume juvenile hake (*Merluccius hubbsi*). All over the shelf they take rock cod, *Patagonotothen ramsayi* (Ivanovic, 2010), and while foraging on and migrating along the shelf break and continental slope between 44°S and 52°S the squid fed on myctophids, particularly *Gymnoscopelus nicholsi* (Haimovici et al., 1998).

Throughout the species range, cephalopods are of less importance in the diet and comprise mostly juvenile conspecifics (from 19 to 70% of the predator ML) and *Doryteuthis* spp: *D. sanpaulensis* north of 40°S and *D. gahi* south of 43°S. Some pelagic tropical and subtropical cephalopod species are occasionally found in the diet off Southern Brazil (Ivanovic and Brunetti, 1994; Santos and Haimovici, 1997; Ivanovic, 2010;).

3.3.2. Temporal Variations

In summer and autumn – the seasons when most food is consumed on the Patagonian shelf – the diet is dominated by *T. gaudichaudi*, the staple food for most of their ontogeny, followed by euphausiids. In winter and spring the biomass of this amphipod species is low (Sabbatini and Alvarez Colombo, 2001) and it is largely absent from the diet in late winter spawners which switch to a mostly euphausiid diet (Ivanovic and Brunetti, 1994). With respect to fish and squid, seasonal changes in diet are minor and reflect seasonal changes in squid size and its distribution throughout the species range.

3.4. Predators

Off Southern Brazil *I. argentinus* is an important prey of wreckfish, *Polyprion americanus*, bigeye tuna, *Thunnus obesus*, and swordfish, *Xiphias gladius* and some marine mammals including dolphins, *Delphinus sp.*, sperm whales *Physeter macrocephalus*, dwarf sperm whales *Kogia brevirostris* and subantarctic fur seals *Arctocephalus tropicalis*. It has also been found in stomachs of demersal fishes including *Merluccius hubbsi*, *Pagrus pagrus*, *Pomatomus saltatrix*, *Trichiurus lepturus* and *Squatina spp* as well as in mako shark *Isurus oxyrinchus* and sailfish *Istiophorus spp.* (Haimovici et al., 1998; Santos and Haimovici, 2002).

On the Patagonian shelf *I. argentinus* is an important part of the diet of common hake (*M. hubbsi*), in which it represents > 50% of annual food intake (Angelescu and Prenski, 1987). It is also consumed by hoki, *Macruronus magellanicus* and red cod, *Salilota australis* (Haimovici et al., 1998). In turn, juvenile hake is prey for *I. argentinus* of the South Patagonian stock. Both species forage on the Argentine anchovy (*Engraulis anchoita*) so they are mutual predators, prey and competitors. This situation exists from April to June in the northern Patagonian shelf, and between January and July in the south (Roper et al., 2010). *Illex argentinus* is also intensively fed on by dogfish, *Squalus acanthias* in which it represents >40% of food by weight and occurrence (Koen Alonso, 1999; Koen Alonso et al., 2002). Various species of penguin, albatross, some petrels and a range of seals and dolphins are also occasional predators (Koen Alonso, 1999; Cherel et al., 2002; Xavier et al., 2002; Clausen and Pütz, 2003;).

In the vicinity of the Falkland Islands, the southern Patagonian stock has few important predators because squid have grown to a large size before they arrive there. Occasionally they are found in stomachs of hakes, Patagonian toothfish *Dissostichus eleginoides*, kingclip *Genypterus blacodes* and sharks. The most common predator in this region is red cod, *Salilota australis*, for which it represents about 3% of prey by numbers and is found in 10% of stomachs (Laptikhovsky et al., 2010). It is estimated that the total contribution of *I. argentinus* by weight to the diet of Patagonian predatory fishes is between 40 and 75% (Roper et al., 2010).

3.5. Parasites and Parasitic Relations

Parasitological studies of *I. argentinus* have been carried out over most of the species range from southern Brazil to the southern part of the Patagonian Shelf including the slope and adjacent ocean and these studies have included intraspecific ecological groups and all ontogenetic stages (Threlfall, 1970; Gaevskaya and Nigmatullin, 1978; Gaevskaya et al., 1986; Carvalho and Nigmatullin, 1998; Haimovici et al., 1998; Nigmatullin, 1989; Nigmatullin and Sardella et al., 1990; Shukhgalter, 1990, 2010; Shukhgalter, 1992; Vidal and Haimovici, 1999; Gonzalez and Kroeck, 2000; 2008). These studies have identified 21 species and their larval forms. The known parasites are Aggregata sp.; helminthes including tetraphyllidean cestodes: *Pelichnibothrium speciosum* l., *Phyllobothrium* sp. l. II, *Phyllobothrium* sp. l. III, *Scolex polymorphus*, *Scolex pleuronectis*, *Dinobothrium* sp. l. and tetrahyarchideans: *Hepatoxylon trichiuri* l., *Nybelinia lingualis* l. Trematodes: Didymozoidae gen.sp. mc, *Derogenes varicus* (adult), *Hirudinella ventricosa* juv.; nematodes *Anisakis*

simplex l., *A. physeteris* l., *Porrocaecum* sp.l., *Contracaecum* sp.l., *Hysterothylacium* sp. l., *Pseudoterranova* sp. l., *Spinitectus* sp. l., *Ascarophis* sp. l. and *Spirurata* gen.sp. l.

All these parasites occur mostly as larval stages. Other ontogenetic stages of parasites are represented by adult *Aggregata* sp. and *Derogenes varicus* and juveniles of *Hirudinella ventricosa*. All three seem to be accidental parasites and occur very rarely.

Three helminth groups have been recognised on the basis of data on rates of infection (Nigmatullin, 1989, 2008; Nigmatullin and Shukhgalter, 1990, 2010; Sardella et al., 1990; Gonzalez and Kroeck, 2000). The main helminths (defined by a prevalence of > 40-50%) are *Phyllobothrium* sp. l. III (= *S. polymorphus*, *S. pleuronectis*), *Anisakis simplex* l. and metacercaria of Didymozoidae. The second group of helminths (defined by a prevalence of 10-40%) includes *Phyllobothrium* l. II, *Pelichnibothrium*, *A. physeteris* l., *N. lingualis* l. and *Spirurata* gen.sp. l. Rare helminth parasites (defined by a prevalence of < 10%) comprise the rest of the samples that have been obtained. This classification remains conditional (except for *Phyllobothrium* sp. l. III and a third rare group) because there are significant differences between samples from different localities and seasons. *Phyllobothrium* sp. l. III occurs at a high level of infestation (50-100%) in squid of ML > 180-200 mm across the whole species range. There are no differences in rate of infestation between male and female squid of the same size. However, larger adult females show higher infestation rates than adult males.

The first parasite to appear in SPS squid is metacercaria of Didymozoidae that occur in paralarvae and later in juveniles. Infection rate increases from 8.3% (1-3 parasites) in squid of 2.2-6.7 mm ML to 75.5 % (1-15 parasites) in animals of 17-46 mm ML. After migration onto the Patagonian shelf no metacercaria have been found in squid of 180 - 380 mm ML (Vidal and Haimovici, 1999; Nigmatullin, 2008) including spawning aggregation off Brazil (Haimovici et al., 1998). However, dydimozoids were found in adult squid from the local Brazil population in autumn. Because there are no dydimizoids in temperate waters of the Patagonian shelf, in both the SSS and BNS the first parasites appear at the juvenile stage only and those are *Phyllobothrium* sp. l. III, *Pelichnibothrium* and *A. simplex* with total rates of infection of 4-21%. In adults the infection rate reaches 52-62% for both groups, and similar rates of infestation are particular to the SPS (Nigmatullin and Shukhgalter, 1990, 2010).

There are clear geographic trends in helminth fauna and infestation rates. They include: 1) dydimozoid distribution confined to the northern part of the range of *I. argentinus* (Nigmatullin, 2008); 2) absence of *Pelichnibothrium* in the slope and oceanic part of the range; 3) distribution of *A. simplex* in coastal waters; 4) presence of *A. physeteris* in oceanic and slope waters (Nigmatullin and Shukhgalter, 1990, 2010).

There are no major differences in the rate of infestation by helminths through the year - the rate ranges between 55-59% on the Patagonian shelf edge and slope (Nigmatullin and Shukhgalter, 1990). Neither does there appear to be interannual variation in infestation rate based on observations in 1983, 1984 and 1988 on subadult and adult squid (Nigmatullin and Shukhgalter, 1990, 2010).

All helminth parasites found in *I. argentinus* are characterised by broad host specificity. They infect various planktonic invertebrates, micronektonic teleosts and squid at different stages in their life cycle. The squid are secondary intermediates (transport hosts) for these helminths. The final hosts for cestodes are sharks and skates; for didymozoid trematodes: scombroid fishes (mainly tunas), and for nematodes: xiphoid and some other teuthophagous teleost fishes (for *Porrocaecum*, *Hysterothylacium*, *Spinitectus* and *Ascarophis*); marine

mammals for *Anisakis* and *Pseudoterranova* and seabirds for *Contracaecum* (Hochberg, 1990).

4. Fisheries

4.1. Fishing Areas

Illex argentinus has a wide distribution across the Patagonian Shelf and can be classed as a 'straddling stock', i.e. one which is harvested in several nationally controlled regions and high seas waters. The fishing fleet is composed of jigging vessels that use powerful lights to attract squid, and it is possible to measure the spatial distribution of the entire light-fishing fleet using satellite imagery (Rodhouse et al., 2001; Waluda et al., 2002; 2008). Due to the intensity of fishing, changes in the distribution of the fleet can reflect changes in the distribution of *I. argentinus*, and it is possible to interpret the distribution of the fleet over a single fishing season in terms of the known life cycle and migration pattern of the species. Fishing lights are observed towards the north of the region in January, spreading southwards along the shelf-break in February, forming fishing concentrations to the north of the Falkland Islands in April, and dispersing north in early June (Waluda et al., 2002). An analysis of the light-fishing fleet over the period 1993 to 2005 (Figure 1) showed that the fleet occupied a large part of the Patagonian shelf and slope, with areas of consistent fishing effort (defined as in 12-13 years of the study) observed in three distinct regions (a) the high seas region on the shelf edge between 45 and 47° S, (b) the northeast (50° S; 62° W) and (c) northwest (50°S; 60°W) of the Falkland Islands conservation zones (Waluda et al., 2008).

4.2. Fishing Methods

The offshore distribution pattern of the different stocks of *I. argentinus* was responsible for the relatively late start of exploitation by fisheries. In the 1970s, coastal trawlers in Argentina and Uruguay made small by-catches of this squid whilst targeting the traditional hake fisheries. At the end of the decade, some fishing companies started to target aggregations of *I. argentinus* on the Patagonian shelf, achieving annual catches of 73,000 t in 1978 and 122,000 t in 1979 (Csirke, 1987). In 1979 a Japanese research vessel *Shinkai Maru* carried out a major trawl survey of the Patagonian Shelf and estimated a minimum standing biomass of 0.9 million tonnes of the winter-spawning (South Patagonian) stock of *I. argentinus* prior their pre-spawning northward migrations to the continental slope (Sato and Hatanaka, 1983). This survey was the trigger for the development of one of the largest cephalopod fisheries in the world.

In 1980 a Russian trawler surveyed the distribution of *I. argentinus* and found commercial concentrations of squid on the high seas at 45-47°S off the Argentinean EEZ. In the following year, a substantial fleet of trawlers of several (mainly eastern European countries) started commercial exploitation of *I. argentinus* on the high seas, with total annual catches reaching 250-300,000 t.

The fleets followed the ontogenetic migrations of squid on the Patagonian shelf. In January to early March, feeding aggregations were targeted on the shelf at 130-160 m depth, mainly during daytime when squid schools were near the bottom.

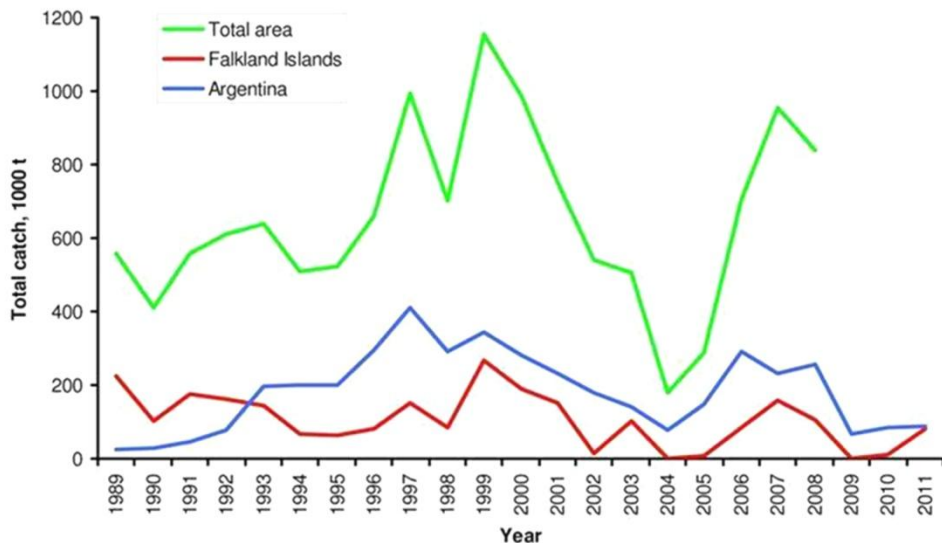


Figure 8. Annual total catch of *Illex argentinus* by fishing zones (Falkland Islands Government, 2012).

In April - June, pre-spawning aggregations were fished at 600-650 m over the continental slope, initially at 47-48°S, then at 45-47°S, and then further north at 42°S at depths of 700 to 750 m. As squid concentrations were well above the bottom, trawlers fished with large pelagic trawls with the ground gear almost touching the bottom and with a vertical opening of 40-50 m.

After 1983, an international fleet consisting of 130-150 large trawlers (including up to 100 from the former USSR) fished for *I. argentinus* on the high seas, achieving total annual catches of up to 700-800,000 t (Figure 8, 9).

The collapse of the Soviet Union and Eastern socialist block heavily impacted on these far seas fisheries, eventually reducing the trawler fleet in the Southwest Atlantic to a few vessels by 2000. Since then, mainly Spanish and Korean trawlers have caught *I. argentinus* in shallow waters (130-160 m) as a main by-catch of the hake fishery. The trawl fishery in deep water no longer exists.

Dense concentrations of the newly discovered resource attracted Asian (mostly Japanese, Taiwanese, Korean and, later, Chinese) jigging vessels to the Southwest Atlantic. A typical jigging vessel was about 70 m long, with a gross registered tonnage of around 1000 t, deploying about 100 jigging lines and 150 jig lights (Figure 10). The vessels worked in the same way as for catching Japanese flying squid *Todarodes pacificus* by attracting both squid and their crustacean prey by lights at night. Typically, each vessel caught 15-20 t of squid per night (exceptionally up to 100 t). Starting in 1984 the jigging fleet grew from several dozen to about 200 vessels.



Figure 9. A catch of *Illex argentinus* caught by trawl (Falkland Islands Government, 2012).



Figure 10. A catch of *Illex argentinus* on board a jigging vessel (Falkland Islands Government, 2012).

Since 1987 the jiggers started to fish under licenses issued by the governments of both Argentina and the Falkland Islands. Jigging for *I. argentinus* proved to be the most economical method both in terms of value of the product and its exceptional quality. Squid caught by jiggers are in pristine condition with intact skin which is very attractive to the Asian markets, whereas those from trawl catches are of much inferior condition usually having a deformed mantle and damaged skin, caused mainly by the fish by-catch in the cod-end.

At the time of writing *I. argentinus* is fished mainly by jigging fleets in Falkland Islands waters (~100 vessels), Argentine waters (ca 50 vessels), and on the high seas by some 20-60 trawlers of the different nations.

4.3. Landings and CPUE

In the 1960s *I. argentinus* was only taken as by-catch from the developing bottom trawl fishery for hake. As the small directed bottom trawl fishery developed in 1973, the total catch remained less than 6,000 tonnes until 1977.

It then increased to 75,000 t in 1978 and to 122,000 t in 1979 - mainly due to the development of a full-scale operation by Argentinean trawlers which transferred from the traditional hake fishery to squid. Japanese and Polish trawlers also contributed to the increase in squid catches in the area at this time (Haimovici et al., 1998). In 1981 the fleet was joined by Soviet trawlers on the high seas. Catches grew steadily after that time but annual catches fluctuated widely. By 1990 the catch had grown to 410,117 tonnes and since then has gradually increased to a record high of 1.153 million tonnes in 1999. Since 2000 the fishery has been very variable with a major failure in 2004-2005 and 2009-2010 (Figure 8). Nevertheless, it is the most important fishery in the Southwest Atlantic and one of three the most important cephalopod fisheries worldwide.

Because stocks of *I. argentinus* fluctuate widely from year to year, so does catch per unit effort in the different fleets. Generally daily catches of trawlers operating on the high seas from December to July are around 10 t day⁻¹ (Figure 11) with a peak between January and March, though in good years some of the largest trawlers might take as much as 40 - 70 t d⁻¹. In Falkland Islands waters jigging vessels normally take 10 - 30 t d⁻¹, whereas trawlers fishing for mixed aggregation of squid and fish in this area catch about 5-8 t/d of *I. argentinus* between March - April as well as 10-30 t/d of miscellaneous fish, mostly rock cod (Figure 11).

There is evidence that the distribution of the fishery is related to mesoscale oceanographic features, for example *I. argentinus* has been shown to be associated with the shelf-break front in Argentine and international waters (Haimovici et al., 1998; Hatanaka, 1988). In Falkland Islands waters higher fishery abundance (catch per unit effort; CPUE) has been observed in thermal gradient areas at the interface of the Falkland Current and Patagonian Shelf waters, with the fishery likely to be targeting pre-spawning/feeding concentrations of squid aggregating in such areas (Waluda et al., 2001b).

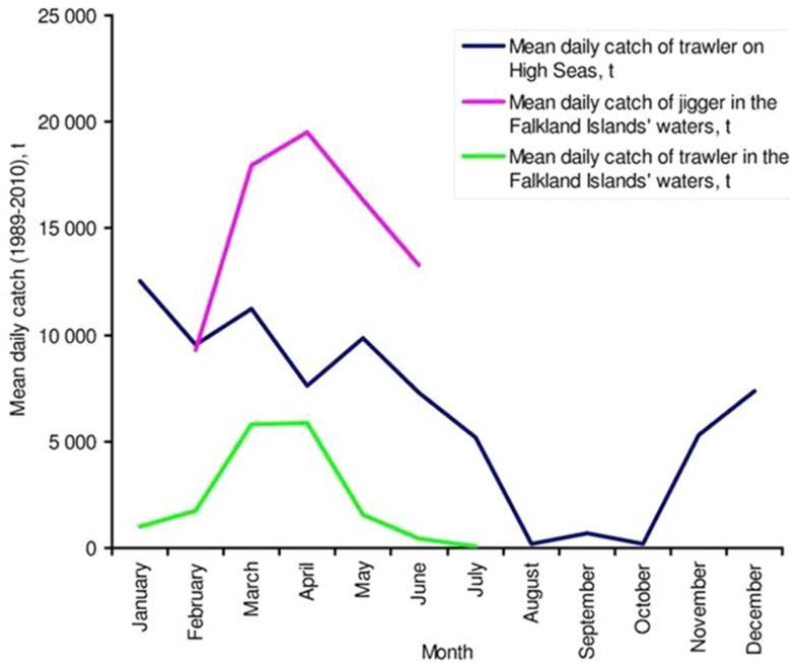


Figure 11. Seasonal changes in *Illex argentinus* CPUEs of different fleets in the Southwest Atlantic (2008-2012). (Falkland Islands Government , 2012).

4.4. Recruitment and Environmental Variability

Oceanographic processes have been shown to be key drivers of variability in squid stocks around the globe, with many species associated with frontal systems, upwelling areas, rings, meanders and streamers (Semmens et al., 2007). Remotely sensed SST (sea surface temperature) data have been combined with *I. argentinus* fishery statistics to explore the relationship between recruitment processes and the physical environment (Waluda et al., 1999, 2001a). In an analysis of environmental variability during the juvenile and adult life history stages, Waluda et al. (1999) found that whilst SST in the Falkland Islands fishing grounds (centered on 48° S; 61° W) during the adult phase of life was not related to variability in catch per unit effort (CPUE, tonnes/vessel) in the fishery, SST in the putative hatching grounds of the northern Patagonian shelf (centered on 36° S; 51° W) during the period of hatching (particularly June and July) was positively correlated with CPUE in the Falkland Islands fishery in the following season (when progeny from the hatching grounds would be exploited by the fishery). This analysis used data from 1987 to 1998 and explained around 41% of the variability in population size over this period, with cooler conditions apparently favouring higher CPUE (Figure 12).

Time series analyses between SST in the South Atlantic and El Niño events in the tropical Pacific revealed teleconnections between the ocean basins with a two year lag between the Pacific and the southern Patagonian shelf (where the fishery is pursued) and a five year lag between the Pacific and the northern Patagonian shelf (where the hatching grounds are located) (Waluda et al., 1999). Population variability in the *Illex argentinus*

population in the South Atlantic seems to be driven, at least in part, by ENSO events in the Pacific.

Waluda et al. (2001a) went on to examine possible relationships between mesoscale oceanography in the hatching area on subsequent recruitment success in the *Illex argentinus* fishery (over the period 1987 to 1999). Using remotely sensed SST imagery at 5 by 5 km resolution they examined variability in mesoscale oceanography during the hatching months of June and July.

These analyses examined the proportion of the inferred hatching area occupied by (1) frontal waters (defined as areas with SST gradients of $\geq 3^{\circ}\text{C}$ over an area of 15 by 15 km) at the interface between the Brazil and Falklands Currents, and (2) waters within the temperature range suitable for hatching (defined as within the range $16\text{--}18^{\circ}\text{C}$; based on the work of Brunetti and Ivanovic, 1992). Higher fishery abundance was found to be associated with a lower proportion of frontal waters (i.e. a weaker confluence front) or a higher proportion of favourable SST waters within the inferred hatching area. The two parameters were found to co-vary and explained around 51 % and 55 % of the variability in CPUE in the Falkland Islands fishery respectively (Waluda et al., 2001a).

The study suggests that retention/transport of eggs and paralarvae in the spawning area close to the shelf is favoured when the confluence front is weak and concurs with the work of Sakurai et al. (2000) who concluded that recruitment is favoured when availability of suitable SST habitat is increased.

Similarly, a positive correlation was found between SST in November over the inferred hatching and early juvenile foraging grounds ($35^{\circ}30'\text{S}$, $53^{\circ}30'\text{W}$ and $36^{\circ}30'\text{S}$, $53^{\circ}30'\text{W}$ respectively) and winter spawning cohort abundance (mean standardized daily catch, t/d) on the high seas in May. Respective coefficient of correlation were $r=0.56$ ($p=0.04$) and $r=0.55$ ($p=0.04$) (Laptikhovsky et al., 2001).

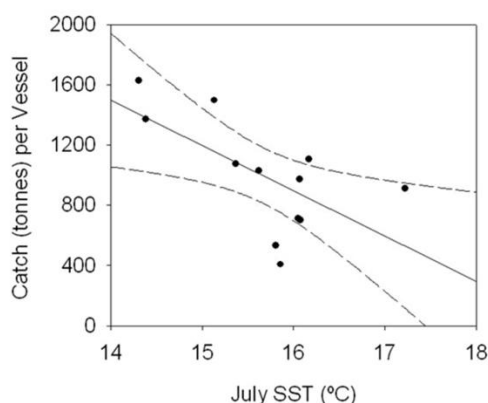


Figure 12. Relationship between CPUE in the *Illex argentinus* fishery around the Falkland Islands and sea surface temperatures in the putative hatching grounds of the northern Patagonian shelf in July of the season prior to the fishery.

Further analyses examined the the response of recruitment processes in six southern hemisphere squid populations (*Dosidicus gigas* in the Southeast Pacific, *Loligo vulgaris reynaudii* in the Southeast Atlantic, *Nototodarus sloani* and *N. gouldi* in the Southwest Pacific and *I. argentinus* and *L. gahi* in the Southwest Atlantic) and basin-scale

environmental indices (the Southern Oscillation Index, SOI and Trans-Polar Index, TPI) (Waluda et al., 2004). *Illex argentinus* CPUE (1987 to 2000) was positively correlated with the SOI during both the spawning/recruitment period (August, October and December) in the year prior to the fishery and during the fishery period (April), and was negatively correlated with the TPI during the fishery period (March) (Waluda et al., 2004). A degree of synchrony was found between processes in the six species, with the SOI apparently having a greater influence during early life history stages and TPI during adult life stages. This suggests a degree of latitudinal separation with juveniles potentially influenced by environmental variability at lower latitudes and adults at higher latitudes (Waluda et al., 2004).

Links between environmental variability and squid abundance (particularly during the early life history stages) may form the basis for predicting recruitment in short-lived species such as *Illex argentinus*. Indeed, it was found retrospectively that the relationship between SST and recruitment described above (Waluda et al., 1999) could have been used to predict fisheries catches in Falkland Islands waters, with very low catches in 2002 related to warm conditions (1.5 °C above average) during the 2001 hatching season (Bostanci et al., 2002).

4.5. Management and Stock Assessment

Assessment of *I. argentinus*, which is a straddling stock, is particularly challenging in the Southern Atlantic. During its ontogenetic migrations, it occurs in the Exclusive Economic Zones of Brazil, Uruguay and Argentina, as well as in Falkland Conservation Zones and on the High Seas at 42°S and 45-47 °S beyond the Argentine EEZ.

Two different methods have been used to estimate abundance on the Patagonian Shelf. Before the current level of exploitation, several biomass surveys were carried out by R/V *Walter Herwig* (1978), *Shinkai Maru* (1978/79) and *Dr Holmberg* (1981/82). Biomass was estimated by the swept-area method assuming the trawl catchability = 1 giving a minimum value. Despite the large range of biomass estimated by different authors using data from these surveys, the most reasonable estimate has is estimated to be between 635,968 t (Otero et al., 1981) and 2,605,000 t (Sato and Hatanaka, 1983). Recently (in late January 2012), the squid pre-recruitment survey by Argentine scientists from INIDEP showed a total biomass of 316,193 tonnes of juvenile SPS *I. argentinus* (1,652 million individuals) (Murias, 2012). To recalculate these numbers into commercial stock estimations, data on squid growth and weight and natural mortality need to be applied.

In 1990, Argentina and the United Kingdom established a bilateral South Atlantic Fisheries Commission (SAFC), with the main aim of exchanging information on *I. argentinus* catches and locations with further recommendations for stock conservation if necessary. Within the SAFC, it was possible for scientists representing both countries to present data on biology, ecology and stock assessments of *I. argentinus* at sessions of the Scientific Sub-Committee. Further, in the Joint Statement between the Argentina and the United Kingdom on 14 July 1999, an agreement was made to enhance cooperation taking into account the relative stability of *I. argentinus* stocks and their economic significance. It was also agreed to co-coordinate fisheries protection and make the necessary multilateral arrangements for the high seas.

The SAFC organized joint trawl surveys of recruitment of the South Patagonian winter spawning stock on the Patagonian Shelf before the start of the fishing season in February.

Abundance and biomass was estimated by swept-area method using Argentinean research vessels.

During the season, stock abundance was estimated by a modified DeLury model (Beddington et al., 1990; Rosenberg et al., 1990) under the assumption that in March and April squid remain in the same area (Southern Patagonian Shelf) with no substantial immigration or emigration. Later, Basson et al. (1996) improved this depletion model by considering the immigration of squid to the fishing ground. It was established that if the Spawning Stock Biomass should fall below the threshold limit of 40,000 t for the Southwest Atlantic, the SAFC should recommend early closure of the *Illex* fisheries both in Argentina and the Falkland Islands. Such early closures were implemented in a number of years. Since 2005 the SAFC has been inactive because the Argentine Government withdrew from meetings and suspended joint scientific activities. This has potentially increased the vulnerability of the stock. Since around 2000 *I. argentinus* recruitment has become more variable, probably reflecting both environmental conditions and the effects of exploitation.

Currently, the Southwest Atlantic region suffers from lack of any effective regional management and conservation of straddling *I. argentinus* stocks because there is no regional fisheries management organisation (RFMO). An RFMO should include all or the majority of countries whose fleets are exploiting those stocks. To date no such organization exists making the Southwest Atlantic unique in having no comprehensive fisheries management programme. Clearly, lack of effective fishery regulation and regional management makes the *I. argentinus* stocks vulnerable to over-exploitation, especially in years of low abundance.

4.6. Interactions between Fisheries and Higher Predators

There has been relatively little research on the role of *I. argentinus* in the diet of higher (air breathing) predators in the South Atlantic though some data have been published by a number of authors (e.g. Koen Alonso, 1999; Cherel et al., 2002; Xavier et al., 2002; Clausen and Pütz, 2003). No attempt has been made to determine the total biomass consumed by seabirds, seals and whales so there is therefore little evidence of the level of competition between fisheries and wildlife. In spite of the ecological significance of the Patagonian Shelf region and, from the human point of view, economically and culturally important species of fishes, seabirds and marine mammals there is at present little evidence on which to base an ecosystem based fishery management (EBFM) approach.

Squid jiggers, which dominate the *I. argentinus* fishery on the Patagonian Shelf and shelf edge, attract relatively few seabirds, so the immediate threat of mortality to albatrosses and petrels is less than from longline fisheries for other species which may cause considerable mortality in the absence of mitigation measures. In fog, jigger lights can attract large numbers of disorientated sea birds and although they may come aboard the jigging vessels they do not generally become entangled with the fishing gear.

Squid jigs descend vertically into the water and are not baited. The catch is brought to the surface snagged by the jigs, they come inboard via mesh covered outriggers and are carried below deck in flowing seawater for processing so there is little or no material from the catch for seabirds, or other higher predators to feed on. Furthermore the catch is mostly frozen whole on board so there are no discards of offal for seabirds to scavenge.

The jigger fishery targeting *I. argentinus* seems to be a rare example of a fishery which causes low incidental mortality of higher predators – including fish. However, the annual level of removals represents a major extraction of biomass from the Patagonian Shelf ecosystem so there may be a hidden impact that cannot be determined given the current level of knowledge.

Conclusion

Since the start of large-scale exploitation of *Illex argentinus* in the Southwest Atlantic in the 1980s a considerable body of knowledge on the biology and ecology of the species has been published. Progress has been made in understanding the environmental drivers of recruitment variability in this and other species of ommastrephid that are commercially exploited. Nevertheless, predictions based on environmental factors alone, are not yet a part of management of the fishery and further work is required to develop this potentially valuable approach to the rational exploitation of the stock. Better understanding of the different populations of *I. argentinus* would be aided by improved knowledge of their genetic structure and by comprehensive data on larval distribution in time and space. Understanding the role of *I. argentinus* in the diet of the higher predators that forage on the Patagonian Shelf and shelf edge would enable an ecosystem approach to fisheries management to be adopted. Finally, sustainable exploitation of the stock would be improved by the establishment of a Regional Fisheries Management Organisation in the Southwest Atlantic.

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***Todaropsis eblanae*, Lesser Flying Squid**

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Abstract

This article presents an updated review of the biology, ecology and fisheries of ommastrephid squid *Todaropsis eblanae*, and the first preliminary identification of the early life stages (Rhynchoteuthion) is also given. Estimations from growth increments in statoliths show average growth rates of 0.30 mm mantle length (ML) day⁻¹ in males and 0.67 ML day⁻¹, and a life span of one year. The species is an intermittent terminal spawner. A total fecundity of 122,129 ± 18,270 oocytes was calculated. The hatching season extends all year round with peaks varying according to latitude. Spawning grounds are still unknown. *T. eblanae* exhibits a very disjunctive geographic distribution. The existence of at least 3 genetically isolated populations in the Eastern Atlantic has been shown. It is a demersal species associated with sandy and muddy bottoms mainly in the lower sublittoral (30 m) and upper bathyal (850 m) over the continental shelf. The abundance indices of *T. eblanae* off NW Spain were significantly related with upwelling events. The species is an opportunistic predator, taking a wide variety of prey. Cannibalism has frequently been recorded. Toothed whales, dolphins, fish and other cephalopods are most important predators. At least three genetically isolated populations exist in the Atlantic Ocean: South African and Mauritanian populations being genetically distinct both from one another and from European populations. *T. eblanae* is taken mainly as bycatch in trawl fisheries throughout its distributional range. It is also caught by artisanal fisheries in the Mediterranean and in the eastern Atlantic. No official separate statistics are available for this species. Recruitment extended all year round, with a peak in autumn-early winter. Juveniles recruit to the fishery at approximately three months of

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age. Presently there are no measures of management or stock assessment for this species in any place of its area of distribution.

1. Introduction

The lesser flying squid *Todaropsis eblanae* (Ball, 1841) belongs to the family Ommastrephidae Steenstrup, 1857. The ommastrephid squids are the most abundant, widely distributed and ecologically active family of cephalopods (Roper et al., 2010). Members of this family range from small (about 100 mm mantle length; ML) to large (about 1000 mm ML). Some are commonly known as "flying squid" due to their ability to glide over the ocean surface (Young et al., 2010).

The maximum recorded size of *T. eblanae* was 290 mm mantle length (ML) for females and 220 mm ML for males in the North Sea (Roper et al., 2010). The mantle is almost cylindrical, robust and stout.

The species has a large and broad head with four nuchal folds on posterior part or neck (Figure 1). Thick lateral funnel-adductor muscles connect lateral edges of funnel with head near its ventral surface. The funnel locking-cartilage has the form of an inverted-T (Figure 2). Its funnel groove has neither foveola nor side pockets, and because of this character it was included within the subfamily Illicinae Posselt, 1891 (e.g. Nesis, 1982; Guerra, 1992; Hernández-García and Castro, 1995; Wormuth, 1998). However, the phylogenetic study carried out by Roeleveld (1988), based on a number of different structures (but rely heavily on the structure of the hectocotylus) placed *Todaropsis* in a branch joint to *Nototodarus*, and considered a member of the subfamily Todarodinae Adam, 1960 (Young and Vecchione, 2008). Roeleveld (1998) reviewed the importance of the funnel groove and reassessed the placement of this species in the subfamily Illicinae. Nigmatullin (1992) based on the analysis of 18 morphological characters, considered that *T. eblanae* should be place within a new monotypic subfamily (Todaropsinae), and that *T. eblanae* is more closely related to the Todarodinae than to the Illicinae, without, however, belonging to either subfamily (Laptikhovsky and Nigmatullin, 1999; Nigmatullin and Laptikhovsky, 1999; Nigmatullin et al., 2003).

This peculiar isolation of *Todaropsis* Girard, 1890 with respect to the other species of the family is supported to a degree by the genetic study carried out on 16 ommastrephids species by Yokawa (1994). Young and Vecchione (2008) support the inclusion of *Todaropsis* within Todarodinae, together with *Martialia* Rochebrune and Mabile, 1889, *Todarodes* Steenstrup, 1880, and *Nototodarus* Pfeffer, 1912, even though it differs from the other genera in the absence of foveola, and in some characters of the hectocotylus.

The fins of *T. eblanae* are broad, and its anterior border is more convex than the posterior one; fins length is less than 50% of dorsal mantle length (ML), and the combined fin width is almost equal to 90% of ML (Figure 1).

This external character, joined with the number of sucker rows in the dactylus of the club (4 in *T. eblanae* and 8 in *Illex coindetii*) allows them to be easily distinguished from *Illex coindetii*, which is frequently caught together in trawl fisheries. Hectocotilization is also different in the two species (Guerra, 1992; Roper et al., 2010; see more details in the section 2.3).

There is a considerable amount of research on the biology, ecology and fisheries of the species of ommastrephid squids (see Boyle and Rodhouse, 2005), but it can be said that *T. eblanae* is between the moderately studied ones, since there are many bio-ecological aspects that are still poorly understood.

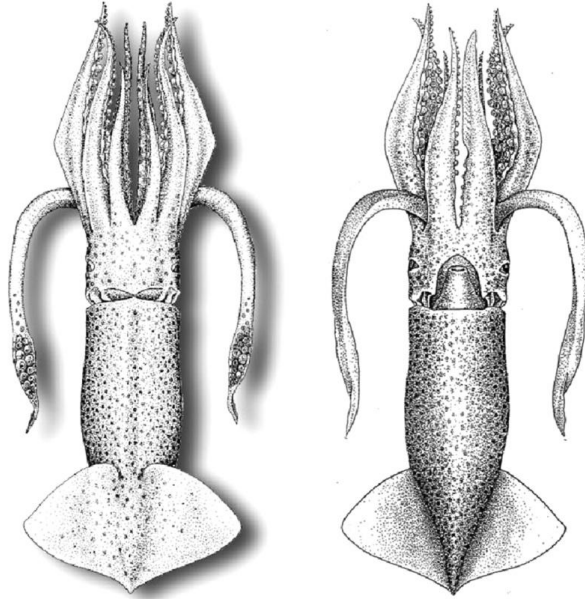


Figure 1. *Todaropsis eblanae*. Drawings showing dorsal and ventral views of an adult squid (from Guerra, 1992).

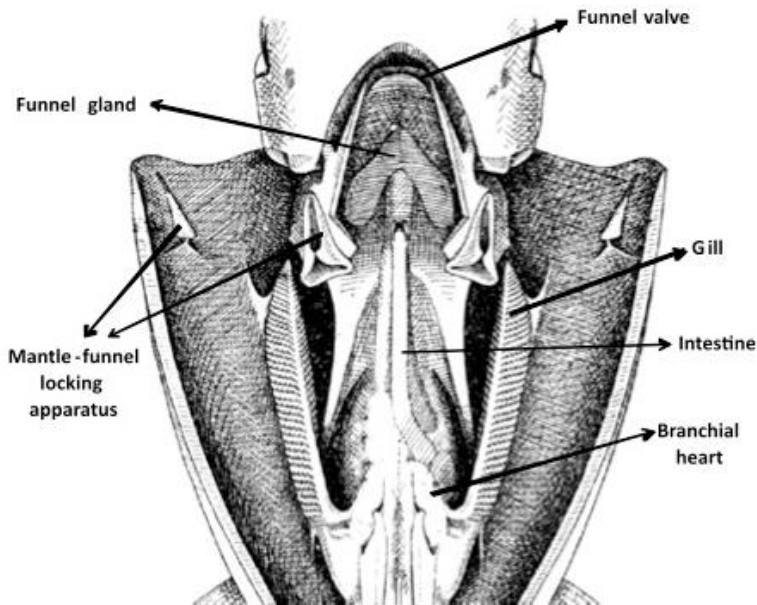


Figure 2. Half-grown female of *Todaropsis eblanae* with opened mantle (from Naef, 1923).

2. Life History Biology

2.1. Early Stages

To date, no *in situ* observation on egg deposition are available, although they probably are laid in a large floating masses, as observed for many other ommastrephids in the natural environment and in captivity (Rasero, 1996; Roper et al., 2010.) The greatly enlarged nidamental glands of mature females supported this hypothesis. The oocytes of mature females vary in size between 0.8 and 2.5 mm along their principal axis with a mean of 1.2 mm in West African waters (Laptikhovsky and Nigmatullin, 1999) and in the Mediterranean Sea (Mangold-Wirz, 1963), and a mean of 1.57 mm in Scottish waters (Hastie et al. 1994), and from 1.0 to 1.8 mm in Galician waters (Rasero et al., 1995; Rasero, 1996) In consequence, the hatchlings size of *T. eblanae* should measure between 0.4 and 0.8 mm mantle length (ML). The duration of embryological development is unknown. As all the ommastrephid squids, *T. eblanae* has a distinctive paralarval form, the “rhynchoteuthion”, characterized by fusion of the tentacles into a “proboscis” (Figure 3). However, the characteristics of the paralarval stage of this species were not defined in the workshop organized by the Cephalopod International Advisory Council (CIAC) held at the Laboratoire Arago, Banyuls-sur-Mer, France, 17-28 June 1985 (Wormuth et al., 1992), and presently the distinctive characters of the rhynchoteuthion of *T. eblanae* have not been described.

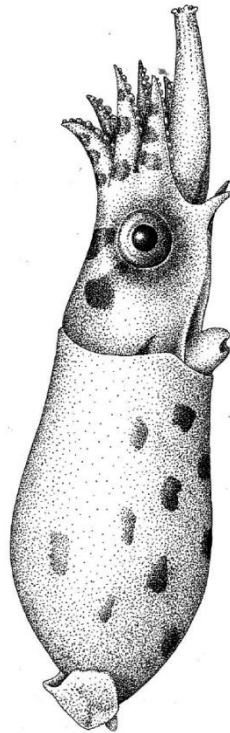


Figure 3. *Todaropsis eblanae*. Lateral view of a characteristic ommastrephid squid paralarvae, rhynchoteuthion (from Guerra, 1992).

During several cruises to capture zooplankton carried out in Galician waters (NE Atlantic) two types of rhynchoteution stages were caught. One of them shares all characters of *I. coindetii* newly hatched obtained by Villanueva (2011) by in vitro fertilization. The other, most probably *T. eblanae*, although an accurate identification should be done to confirm this fact, showed the two dorsal pairs of arms (I, II) present but short; III slightly larger, and IV very short. Tentacle primordia were fused in the characteristic proboscis of this stage. In a paralarvae ranging from 1.36 to 2.03 mm ML, the proboscis was very short (24-28% ML) and wide, and length did not exceeded very much the length of the longest arm. However, as this organ is very retractile precaution should be taken into account considering that index as a valid taxonomical character. On the tip of the proboscis there were six suckers of similar diameter and two central ones slightly wider. The lateral proboscis suckers were not enlarged.

The funnel was very large and surpasses the medium line of the eyes. The fins are very small (15-16 % mantle width). No ocular or visceral photophores were observed. Finally, the external surface of the mantle shows a mosaic-like characteristic epithelial sculpture in fresh material (Villanueva per. com.).

2.2. Age and Growth

Maximum mantle length is 290 mm and 220 mm for females and males, respectively in north Atlantic waters (Robin et al. 2002; Roper et al. 2010). Length-weight relationships differ between regions (Table 1). In general, the values of the regression coefficient (b) are lower than 3 in both sexes, indicating an allometric growth pattern. As shown by the study of Belcari et al. (1999) in Italian waters, in mature females the growth is isometric, indicating a change once the maturation process starts.

Males are smaller than females. Growth rates in both sexes are dependent on the season of hatching, and appears to be related with a gradual increase in water temperature during the spawning season (Rasero, 1996).

In Galician waters, the higher growth rates occurred between 0 and 190 days, reaching new maximums at around 240 days in males, and 270 days in females. It is highly likely that this “growth acceleration” (both in ML and, more markedly, in weight) is related to the process of sexual maturation, which takes place between 200 and 280 days. Sexual maturation is a relatively fast process, as observed in other related species. Growth, both in length and weight, fitted a logistic equation. Average growth rates in Galician waters were as follows: 0.30 mm ML day⁻¹ and 0.90 g BW day⁻¹ in males; 0.67 ML day⁻¹ and 2.01 g BW day⁻¹ in females. Growth rates in males were more variable over time than in females, although the latter generally showed higher values, with a maximum increase of 3.5 g BW day⁻¹ at around day 270 (Rasero, 1996).

French fishery data suggest monthly growth rates of 0.76 cm (males) and 1.22 cm (females) Mantle length instantaneous relative growth rates range from 0.38 to 1.55% for males and from 0.43 to 1.74% for females (Robin et al., 2002.).

Statolith increment counts suggest that *T. eblanae* is likely to have an annual life cycle. Rasero (1996) counts give a range of increments ranging from 174 to 335 in males, and between 162 and 355 in females. The indirect method used by Rasero (1996) validated the hypothesis “one increment = one day”.

Table 1. Length/weight estimations of *Todaropsis eblanae*, based upon the equation $W = aL^b$ where W is body mass, and L is mantle length

Region	a	b	parameter	Reference
Scottish waters	0.0002388 (f) 0.000192 (m)	2.723 (f) 2.777 (m)	W: [g] L: [mm]	Hastie et al. 1994
North Sea	0.0003124 (f) 0.0001311 (m)	2.6597 (f) 2.8541 (m)	W: [g] L: [mm]	Zumholz & Piatkowski, 2005
Bay of Biscay and Celtic Sea	0.33 (f) 0.67 (m)	2.41 (f) 2.15 (m)	W: [g] L: [cm]	Robin et al. 2002
Spanish Atlantic waters	0.0003162 (f) 0.0001066 (m)	2.671 (f) 2.917 (m)	W:[g] L: [mm]	Gonzalez et al. 1994
Portuguese waters	0.0004 (f) 0.0006 (m)	2.65 (f) 2.56 (m)	W:[g] L: [mm]	IPIMAR unpublished data
Western Mediterranean	0.187 (f) 0.163 (m) 0.246 (immature f) 0.039 (mature f) 0.222 (immature m) 0.680 (mature m)	2.57 (f) 2.64 (m) 2.425 (immature f) 3.159 (mature f) 2.473 (immature m) 2.109 (mature m)	W: [g] L: [cm]	Belcari et al. 1999
Eastern Mediterranean	0.000279	2.704	W: [g] L: [mm]	Lefkaditou (unpublished)
Northwest African waters	0.0007	2.5051	W:[g] L: [mm]	Arkhipkin & Laptikhovsky, 2000
South African waters	0.11	2.67	W: [g] L: [cm]	Cooper, 1979

Therefore, ages of individuals sampled ranged from 5 to 11 months. Since only a few of larger individuals were aged in that work, life span of the species may be greater of 12 months. Indirect methods based on length-frequency estimates indicate a longer life span, and as consequence a second year of life cycle was hypothesized (Arkhipkin and Laptikhovsky, 2000; Robin, 2002). By back-calculation, it was estimated that individuals were hatched year round (Rasero, 1996).

2.3. Maturation and Fecundity

The sex ratio of *T. eblanae* is not substantially different from 1:1 (Mangold-Wirz, 1963; Gonzalez et al. 1994; Hastie et al. 1994; Joy, 1989; Arkhipkin and Laptikhovsky, 2000; Rasero, 1996; Robin et al., 2002; Zumholz and Piatkowski, 2005). However, Rasero (1996) observed that maturing and mature males of both areas at the Galician waters (particularly in the west one) were significantly more abundant than females, a phenomenon not observed in

immature individuals. This could be related with a spawning migration of mature females, because spawning could take place in the water column, near the surface. Sexual maturity starts at a larger size in females than in males.

The spawning season probably extends throughout the year, with seasonal peaks varying according to geographical locations (Belcari, 1999). The species spawns mainly during summer in the Catalan sea at the Western Mediterranean (Mangold-Wirz, 1963) and in northern Atlantic waters (Hastie et al., 1994; Robin et al., 2002; Zumholz and Piatkowski, 2005); in spring and autumn in Atlantic waters south of 44 °N (González et al., 1994; Rasero, 1996; Arkhipkin and Laptikovsky, 2000; Hernández-García, 2002). In eastern Australian waters spawning occurs from late summer until early winter (Roper et al. 2010).

Total fecundity in mature females varies geographically, being in western Mediterranean up to 10,000 mature oocytes (Mangold-Wirz, 1963), between 4,500 to 28,000 in Scottish waters (Hastie et al., 1994), and 43,000 to 275,000 oocytes in West Africa (Laptikhovsky and Nigmatullin, 1999). The highest figure given by latter authors is likely to result of counting oocytes of all size present in the ovaries, whereas the previous authors neglected oocytes of very small size. The number of eggs spawned per female ranges from 3,600 to 34,400 (in the oviduct) off Northwest Africa (Laptikhovsky and Nigmatullin, 1999) and from 355 to 13,157 (mature eggs) in Scottish waters (Hastie et al. 1994.) Rasero (1996), counting all type of oocytes present in mature females, estimated an average 993 mature oocytes per gram of oviduct. The mean number of mature oocytes in the oviducts was 12,167. This is likely a good estimate of the number of eggs in each egg mass, coinciding with the previous estimates. Total fecundity of $122,129 \pm 18,270$ oocytes was calculated by Rasero (1996), which is in more agreement with the figure estimated by Laptikhovsky and Nigmatullin (1999) than with the ones calculated by Mangold-Wirz (1963) and Hastie et al. (1994). Immature oocytes are pale yellow in colour; while mature oocytes are bright orange (Rasero, 1996; Roper et al. 2010). Evidence suggests that: a) energy for egg production is taken directly from food, rather than from stores products; and b) the glycogen reserves in the gonad increased significantly, suggesting that the glycogen has an important role in maturation process of this species (Rosa et al., 2005).

In Galician waters, the percentage of the nidamental glands relative to total body weight (BW) of mature females ranged from 6.69 to 16.42%. Oviducts percentage in relation to BW of mature females varied between 0.20 and 7.21 %, ovaries ranged from 1.43 to 8.61 female BW. And the weight percentage of the entire reproductive system of mature females ranged from 6.83 to 30.04 %, with a mean and standard deviation of $18.90 \pm 4.14\%$ of the female BW (Rasero, 1996).

The average number of spermatophores in the Needham's sac is around 100 with a maximum of 269 in Northwest African waters (Hernández-García and Castro, 1995) and 12-130 (mean= 60) in Scottish waters (Hastie et al. 1994.) The number and the length of spermatophores increase with the size of the males. Spermatophores length ranges between 11 and 30 mm.

Estimates of the size at maturity in different areas (Gonzalez et al., 1994, Hastie, 1994; Rasero, 1996; Belcari 1999; Zumholz and Piatkowski, 2005) range between 120 to 131 mm ML and from 140 to 200 mm ML for males and females, respectively.



Figure 4. *Todaropsis eblanae*. Drawings and photo showing the hectocotylized arms of a mature male.

Spermatophores in *T. eblanae* are deposited during the copulation in the buccal membrane of the females, generally in ventral part, in variable numbers. The sperm is transferred to a few (6-8) spermatecae placed also in the ventral region of the buccal membrane (Adam, 1952; Mangold, 1987; Joy, 1989; Rasero, 1996). There is no available information on whether exists or not a nuptial courtship before the copulation, and how it is carried out (Rasero, 1996).

Sexual dimorphism exists in mature individuals of this species. Mature males of *T. eblanae* have the left and the right ventral arms (IV) hectocotylized, right specially so (Figure 4); the right is longer and larger than the left and has a double row of slender, conical papillae and expanded protective membrane distally; the proximal quarter of each arm IV has 4 or 5 enlarged cushion-like trabeculae and a wide protective membrane (having a saw-like or comb-like appearance) that have attenuate supports that extend to the arm tip; dorsal and ventral distal right arm trabeculae, sucker stalks and suckers are modified by enlargements or reductions (Roper et al. 2010).

However, as observed by Adam (1952), Guerra (1992) and Rasero (1996) these enlarged cushion-like trabeculae are 7-9 in each arm. These structures develop as the animal matures sexually, becoming hard and turning black progressively, acquiring a characteristic form, that some authors have termed bractae (Adam, 1952; Guerra, 1992). *T. eblanae* is the only cephalopod that possesses this type of structure. Their function is presently unknown, but it is likely that they play a role in copulation. Rasero (1996) has proposed that the males of *T. eblanae*, like other ommastrephids, can copulate several times; thus, it is possible to think that after the spawning of every mass of eggs follows a new copulation, as it was observed in *Illex argentinus* (Laptikhovski and Nigmatullin, 1992). Then, the bractae might be used by the new male to withdraw the tunics of empty spermatophores, or, even sperm from another male, in order to leave a site for its own sperm. This behaviour has been observed in other cephalopods such as *Sepia officinalis* (Guerra, 2006). Although this is speculative, the breaks and tears frequently observed in buccal membrane of fecundated *T. eblanae* females supports violence during the copulation events, and potentially the removal of spermatophores (Rasero, 1996). The species can be considered as an intermittent terminal spawner with

relatively low fecundity (Rasero et al., 1995; Rasero, 1996; Rocha et al., 2001). The darkening of the beaks in this species seems to be related with the maturing process, which take place over a very short period in the life of the squids (Hernández-García, 2003). Spent females are rarely found, which suggest that the degeneration process after spawning is fairly rapid. Males copulate several times, while spermatophores continue to be produced for further mating (Rasero, 1996). The hatching season of this species extends from October to March in British waters (Hastie et al., 1994; Collins et al., 2002) and from March to July with a peak in May in Northwest African waters (Laptikhovsky and Nigmatullin, 1999). In Galician waters, hatching season extends all year round, although there is a peak at the end of the summer and the beginning of autumn (Rasero, 1996). Spawning grounds are still unknown. One possible location identified is in the north-western Iberian waters, where paralarvae specimens matching the spawning season of *T. eblanae* have been found during several year plankton cruises (Rocha et al., 1999; Moreno et al., 2009).

3. Ecology

3.1. Distribution and Abundance

T. eblanae exhibits a very disjunctive distribution (Figure 5), including the entire Mediterranean Sea and the Eastern Atlantic Ocean, from 61°15'N to 36° S, including the British Isles; western Indian Ocean (Saya de Malha and Nazareth Banks, Mascarene Ridges); western Pacific Ocean, South China Sea and Australian waters: the Timor Sea (northern Australian coast), along the western and eastern Australian coasts, to Tasmania on the eastern side (Zumholz and Piatkowski, 2005; Roper et al. 2010).

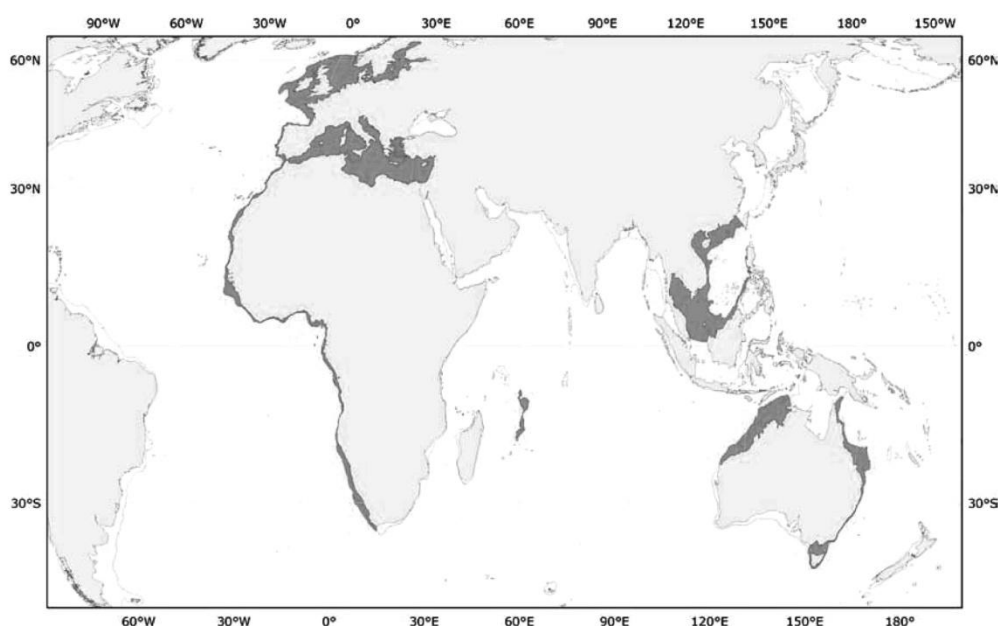


Figure 5. Geographical distribution of *Todaropsis eblanae*.

A distinct population seems to occur in the Southwest Pacific (Lu, 1982) and the Southwest Indian Oceans off Australia (Nesis, 1979). Recent studies on the species from the Atlantic and the Mediterranean indicated the existence of at least 3 genetically isolated populations in the Eastern Atlantic (Dillane et al., 2005).

T. eblanae is a demersal species associated with sandy and muddy bottoms mainly in lower sublittoral and upper bathyal over the continental shelf, not ascending to the surface or approaching the shore. It occurs within a temperature range from 9-18°C and inhabits a wide range of depths (Guerra, 1992; Roper et al., 2010). In the Mediterranean, it has been observed at depths between 200 and 600 m in the western area (Quetglas et al. 2000), from 30 to 700 m in Italian waters (Belcari and Sartor, 1993; Belcari 1999), while in Hellenic seas it has been recorded from 100 to 850 m, being more abundant on the upper slope of regions with steep waters (Lefkaditou, 2007, Katsanevakis et al., 2008).

3.2. Migrations

Like it was previously said, unlike other ommastrephid species, there is no evidence that *T. eblanae* regularly ascends to the surface or approaches shorelines (Hastie et al. 2009). This species is probably the least mobile of the ommastrephid squids in terms of migratory habits and is more likely to behave like the neritic loliginid squid species rather than the sympatric ommastrephid species *Illex coindetii* and *Todarodes sagittatus* (Lordan, 2001; Roper et al. 2010). However, sexes and size distribution at different depths were significantly different in Galician waters, being evident that there is a tendency to find small individuals in shallow waters, and larger sizes at greater depths, which suggest that *T. eblanae* undergoes bathymetric migrations throughout its ontogenic development, at least in the phase from recruitment through to sexual maturity (Rasero, 1996).

The abundance indices of *T. eblanae* from 21 cruises off north-western Spain (30-500 m depth) are significantly related with the upwelling index, calculated in the basis of the wind direction and intensity (Rasero, 1966, Rocha et al., 1999). This positive relationship might be due to the increased survival rates of hatchlings and pre-recruits when abundance and availability of prey increase, as consequence of higher productivity caused by seasonal upwelling. These conclusions are confirmed by the results achieved by means of 57 plankton cruises carried out during a 19-year research in Portuguese waters (Moreno et al., 2009).

The species is scarce in the northern North Sea, around Shetland and just off the Scottish waters, although huge aggregations may occur. These historical phenomena may be linked to hydrographical anomalies such as incursions of warm high salinity Atlantic seawater into the North Sea (Hastie et al., 1994).

3.3. Feeding Ecology and Behavior

In Galician waters (NW Atlantic) a total of 21 different prey items were identified in animals ranging from 34 to 222 mm ML: including teleosts (79%), crustaceans (10.5%) and cephalopods (10.5 %). A substantial fraction of the diet of this *T. eblanae* comprised species of commercial interest in the Galician trawl fishery, with particularly high occurrence of the blue whiting *Micromesistius poutassou*, which alone accounted for almost half (49%) of the

diet (Rasero, 1996; Rasero et al., 1996). The diet of this species in other geographic areas of the Atlantic Ocean and the Mediterranean Sea was composed of similar species which, in decreasing order of importance, were fish (myctophic, clupeid and gadoid), crustaceans and cephalopods (Lordan et al., 1998; Zumholz, 2000; Hernández-García, 2003; Zumholz and Piatkowski, 2005; Form and Oelschlägel, 2004; Vafidis et al. 2008, Hastie et al. 2009).

T. eblanae is an opportunistic predator, taking a wide variety of prey, particularly the most abundant in its habitat. The absence of sympatric benthic organisms in stomach contents indicate that this species feeds mainly in the water column (Roper et al., 2010). No significant seasonal changes were observed in the diet of this species, nor were there any significant differences between sexes (Rasero, 1996). However, the diet was considerably different off the northern and western coast of Galicia, with a particularly high occurrence of blue whiting in the north, and a greater abundance of crustacean in the west (Rasero, 1996). In the central East Atlantic, two different results were found: a) immature individuals fed mainly on fishes (54.54%), decapod crustaceans (43.72%) and cephalopods (1.74 %), while mature specimens fed less on fishes (47.28 %) and decapods (40.77%) and more cephalopods (11.94%) (Hernández-García, 1992); and b) the importance of fish in the diet increased with the squid size, while crustaceans in adults was less important and cephalopod did not change significantly. On the contrary, the diet of males was characterised by slight increase of crustacean importance with the squid size (ca. 7%). The importance of fish and cephalopods is slightly reduced in maturing and mature squids (Hernández-García, 2003). Cannibalism has frequently been recorded, mainly associated with high concentrations of conspecifics and/or scarcity of commonly available prey (Rasero, 1996; Zumholz, 2000; Form and Oelschlägel, 2004; Vafidis et al., 2008; Hastie et al., 2009; Roper et al., 2010.)

A high proportion of cephalopods were found in the diet of immature individuals from the western continental shelf of Galician waters, with an important incidence of cannibalism. It was also observed that the small sized individuals consume large amounts of small teleosts, but not blue whiting, whereas this fish is the basic food for large individuals (Rasero, 1996).

Values of food ratio, expressed as percentage of squid weight, were similar for both areas in Galician waters, although they were slightly higher in the north. In the smaller specimens the food ratio range varied from 11 to 14% in weight, being 5-6% in specimens weighing over 300 g. (Rasero, 1996).

In smaller individuals the maximum weight of prey was roughly equal to predator weight. In predators over 100 g, a stabilization of their maximum prey size was observed. *T. eblanae* almost never captured prey larger than 100g, although larger preys were available in the habitat (Rasero and Castro, 1995). It seems that the maximum sizes would be sufficient to fill the stomach capacity of *T. beanie* of any size. This leads to the conclusion that this species does not ingest prey completely, and does not need catch larger prey, since this would involve a higher energetic cost, whereas the yield obtained would be restricted by the stomach capacity (Rasero and Castro, 1995; Rasero, 1996).

3.4. Predators

Toothed whales and dolphins are considered to be the most important predators of this species, which is also preyed on by birds, fish and cephalopods (Table 2). The only identifiable squid remains in the stomach contents of predators are very frequently beaks.

Table 2. Main predators of *Todaropsis eblanae*

Predators		References
Mammals	Common dolphin (<i>Delphinus delphis</i>)	Pascoe, 1986
	Bottlenose dolphin (<i>Tursiops truncatus</i>)	Santos et al. 1997; Blanco et al. 2001
	Risso's dolphin (<i>Grampus griseus</i>)	Clarke and Pascoe, 1985; Blanco et al 2006
	Bottlenose whale (<i>Hyperoodon ampullatus</i>)	Santos et al. 2001
	Sperm whale (<i>Physeter macrocephalus</i>) Spotted dolphin (<i>Stenella attenuata</i>) Cape fur seals (<i>Arctocephalus pusillus pusillus</i>)	Hastie et al. 2009 Hastie et al. 2009 de Bruyn et al. 2003
Birds	Great albatross (<i>Diomedea</i> spp.) Sooty albatross (<i>Phoebetria fusca</i>)	Hastie et al. 2009 Hastie et al. 2009
Fishes	Blue shark (<i>Prionace glauca</i>)	Clarke and Stevens, 1974
	Sleeper shark (<i>Somniosus</i> spp.)	Hastie et al. 2009
	Shortfin mako shark (<i>Isurus oxyrinchus</i>)	Hastie et al. 2009
	Portuguese shark (<i>Centroscymnus coelolepis</i>)	Hastie et al. 2009
	Smooth hammerhead (<i>Sphyrna zigaena</i>)	Hastie et al. 2009
	Longnosed lancetfish (<i>Alepisaurus ferox</i>)	Lipinski et al. 1992
	Yellowtail amberjack (<i>Seriola lalandi</i>)	Lipinski et al. 1992
Cephalopods	Cape dory (<i>Zeus capensis</i>) Albacore (<i>Thunnus alalunga</i>) Swordfish (<i>Xiphias gladius</i>) Conger eels (<i>Conger conger</i>)	Meyer and Smale, 1991 Hastie et al. 2009 Hernández-García, 1995; Hastie et al. 2009 Xavier et al. 2010
	Clubhook squid (<i>Onychoteuthis banksii</i>)	Hastie et al. 2009

This was the case, for example, in the study undertaken by Xavier et al. (2010) in order to know the trophic relationships of the conger eels (*Conger conger*) from the north-east Atlantic waters. The only squid found in the stomach contents of that fish was *T. eblanae* (1.1% in numbers and 2.3% in mass). That prey was identified from its mandibles, and the size estimations were carried out using the relationships between the mantle length (ML) and the body mass (M) and the lower rostral length (LRL), which were previously calculated by the authors. This type of information is very useful for studies of trophic ecology. The allometric equations for *T. eblanae* were taken for these authors from relationships based on individuals caught in Algarve waters, and they are as follows:

$$\text{ML (mm)} = 5.673 + 22.593 \text{ LRL (mm)}; r^2 = 0.79 \text{ (N: 89, ML: 55 - 147 mm)}$$

$$\text{Ln M (g)} = 2.507 \text{ Ln (LRL)} + 0.778; r^2 = 0.85 \text{ (N: 89; M: 14 - 205 g)}$$

Zumholz and Piatkowski (2004) found no morphological differences between the beaks of males and females of *T. eblanae* from the North Sea, therefore equations were calculated for both sexes. The observed equations for lower rostral length (LRL in mm) against both dorsal mantle length (DML in mm) and wet body mass (BM in g) in the investigated size window (ML= 40 mm - 190 mm, LRL = 1.7 - 6 mm) were: DML= 32.528 LRL – 4.541; $r = 0.943$ and BM= 2.9042 LRL 2.724; $r = 0.955$.

3.5. Parasites

T. eblanae has been found to host six species of helminthes, three tetraphyllidean cestodes (*Phyllobothrium* sp., *Pelichnibothrium speciosum*, *Dinobothrium* sp.), two trypanorhynchidean cestodes (*Nybelinia yamagutii*, *Nybelinia lingualis*), and one ascaridoid nematode (*Anisakis simplex* B) (Smith, 1984; Pascual et al., 1996 a, b; Pascual et al., 1999). *T. eblanae* is the most important paratenic host for *Anisakis* (Abollo 1998, 2001). The copepod *Pennella* sp. (Pascual et al. 1997) and isopods have also been recorded in this species (Pascual et al. 2002.) Parasitism of *Penella* sp. implies about 2.1 and 8.1% of the variation in condition of ommastraphid squids in Galician waters, reducing the condition of *T. eblanae* over 21.1%. Pascual et al. (1998b) also estimated that the reduction in biomass of infested squid were 527 tons for the period 1980-1991, which signified a consistent annual economic loss for the fishery sector, demonstrating that parasitism is not only an important zoonotic problem but an important economic problem as well.

4. Fisheries

4.1. Stock Definition and Fishing Areas

Using morphometric analyses, Rasero (1996) concluded that there were no indications of different populations or stocks of this species off the coast of Galicia. At least three genetically isolated populations exist in the Atlantic Ocean, South African and Mauritanian populations being genetically distinct both from one another and from European populations (Dillane et al., 2005).

4.2. Fishing Methods

T. eblanae is taken mainly as bycatch in otter and pair bottom trawl fisheries throughout its distributional range. Roper et al. (2010) indicate that the species is caught by artisanal fisheries in the Mediterranean and in the eastern Atlantic. In relation to the Atlantic Iberian waters, this species is not captured by any kind of gear handled by boats from small-scale fisheries (Bruno and Rasero, 2008).

4.3. Landings and CPUE

No official separate statistics are available for this species; landings coming from International Council for the Exploration of the Sea areas (ICES, NE Atlantic) and the Mediterranean Sea are pooled for different ommastrephid squid species, including Lesser flying squid (*Todaropsis eblanae*), Broadtail shortfin squid (*Illex coindetii*), European flying squid (*Todarodes sagittatus*) and Neon flying squid (*Ommastrephes bartramii*). Total landings of the short-fin squids from Mediterranean and from Atlantic Iberian waters can be fairly consistent. It is a constant and consistent component of the catches in areas such as the Irish waters, the Galician coasts, the southern Atlantic waters, and in the Sicilian Channel in the Central Mediterranean (Rasero, 1996; Roper et al., 2010). This resource is a minor component of the catch of the French fishery operating in the northern Bay of Biscay and Celtic Sea.

Further north, landings have generally been sporadic. At present, *I. coindetii*, *O. bartramii* and *T. eblanae* are not exploited commercially by U.K. fleets. However, reports from adjacent waters indicate that they can at times be widespread and abundant in the north-eastern Atlantic and may represent a significant potential fishery resource (Hastie et al., 2009).

T. eblanae is less important than *I. coindetii* in French short-fin squid landings (Robin et al., 2002) and more important than *I. coindetii* in Spanish and Portuguese short-fin squid landings, although seasonal variations occurs. Landing of *T. eblanae* from the Spanish fishing fleet operating in the north-eastern Atlantic of the Iberian Peninsula between 1997 and 2004 ranged from 817 to 5159 metric tons (Bruno, 2008.) *T. eblanae* represented the 62% of short-finned squid landings by the Spanish “*baca*” (otter bottom trawl), and *I. coindetii* the 38 %. However, for paired trawl, species composition was opposite: 19% of *T. eblanae* and 81% of *I. coindetii*. Specimen size from otter trawlers ranged between 30 and 120 g, while paired trawlers size of individual varied from 70 to 135 g. On the other hand, on Galicia short-finned yearly average landings data shows a seasonal trend with maximum values in spring (31%) and autumn (26%), while in the Cantabric Sea (Bay of Biscay) a large peak appears in spring representing 45 % of yearly landings (Bruno and Rasero, 2008).

4.4. Recruitment and Environmental Variability

Recruitment extended all year round, with a peak in autumn-early winter (Rasero, 1996; Belcari, 1999; Rocha et al., 1999; Robin, 2002). Juveniles recruit to the fishery at approximately three months of age. *T. eblanae* is taken throughout the year as by-catch in otter trawl fisheries, and, to a lesser extent, with gill and trammel nets, longlines and jigging at depths of 100-400 m in the Mediterranean, off West Africa and in the Northeast Atlantic. Most catches are made around 200 m depths in north Atlantic (Robin et al. 2002) and between 200 and 800 m in the Italian seas with wide annual fluctuations in abundance (Belcari, 1998; González et al., 1994; Hastie et al., 1994).

4.5. Management and Stock Assessment

Presently there are no measures of management or stock assessment for this species in any place of its area of distribution.

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Chapter VI

***Dosidicus gigas*, Humboldt Squid**

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Abstract

Dosidicus gigas (Humboldt or jumbo squid) (Orbigny, 1835) is the largest ommastrephid squid, reaching up to 1.2m mantle length and 65kg in weight. This pelagic squid is endemic to the eastern Pacific Ocean and is particularly abundant in the highly productive waters of the California and Humboldt Current systems, and the Costa Rica Dome upwelling region.

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The intra-specific population structure of *D. gigas* is complex, since this species quickly responds to environmental variability driven by El Niño and LaNiña events in both current systems by rapidly changing its biological characteristics, such as somatic and reproductive investment. Oocyte development is asynchronous and the potential fecundity averages around 18–21 million oocytes; the maximum value estimated (32 million oocytes) is the largest ever recorded for any cephalopod so far. Hatching occurs between 6 to 9 days after fertilization at 18°C, but temperatures below 15°C and above 25°C do not allow complete embryonic development. *D. gigas* passes through a post-hatching paralarval stage called the rhynchoteuthion and during this stage the two tentacles are fused into a well-developed proboscis. During the paralarval and subsequent juvenile stages Humboldt squid have a monthly growth rate of up to 80 mm in mantle length, and grow up 60 mm per month in the later stages. This is the highest growth rate reported for any cephalopod species, and enables this species to reach the reported maximum mantle lengths in a short lifespan (12 to 24 months). Although the lack of population structure across its large range suggests a high level of gene flow and substantial horizontal migration, specific migratory pathways in the Pacific Ocean have not yet been demonstrated. Long-distance migration is an important element in the life-history of Humboldt squid and may be associated with differential growth rates and size and at full maturity.

The recent poleward range expansion of *D. gigas* is likely associated with warmer periods following El Niño/La Niña events, an ongoing expansion of the oxygen minimum zone (OMZ) in the Eastern Pacific, and changing ecosystem interactions including food availability, competition and predation. Humboldt squid feed primarily on small mesopelagic (midwater) fishes, crustaceans, and cephalopods as well as commercially important coastal fishes and squid in the recently expanded range. Typical daily behavior involves vertical migrations from near-surface waters at nighttime to mesopelagic depths above or within the OMZ during the daytime. Whereas the OMZ restricts the depth distribution of many competing vertebrate predators to the upper surface layers due to limited hypoxia tolerance, *D. gigas* circumvents similar restrictions via metabolic suppression. In addition to its critical role both as prey and predator in the eastern Pacific, *D. gigas* is an economically important species and the target of what has recently become the world's largest invertebrate fishery.

1. Introduction

Dosidicus gigas (Humboldt or jumbo squid; Figure 1) (Orbigny, 1835) is the largest ommastrephid squid, reaching up to 1.2m mantle length (ML) and 65kg in weight (Clarke and Paliza, 2000), with one the highest metabolic rates of any animal in the oceans (Rosa and Seibel, 2008, 2010).

Most of the ommastrephid squid species supporting commercial fisheries are found in association with high velocity western boundary current systems but *D. gigas* is an exception to this rule (Rodhouse, 2005, 2008).

It is endemic to the eastern Pacific Ocean and particularly abundant in the highly productive eastern boundary current waters of the California Current and Humboldt Current Systems (Nigmatullin et al., 2001) and the Costa Rica Dome (Anderson and Rodhouse, 2001; Ichii et al., 2002; Waluda and Rodhouse, 2006), where it plays a critical role both as prey (Clarke et al., 1988; Ruiz-Cooley et al., 2004; Abitia-Cardenas et al., 2010) and predator (Markaida and Sosa-Nishizaki, 2003; Markaida, 2006a).

Moreover, the distribution of *D. gigas* has recently undergone a poleward expansion throughout the Eastern Pacific (Nigmatullin et al., 2001; Field et al., 2007; Zeidberg and Robinson, 2007; Keyl et al., 2008). In the northern hemisphere, Humboldt squid suddenly appeared in large numbers after the strong El Niño event of 1997-98 and then disappeared until 2002-03 (Zeidberg and Robison, 2007) when a northward wave of strandings spread up the California coast.

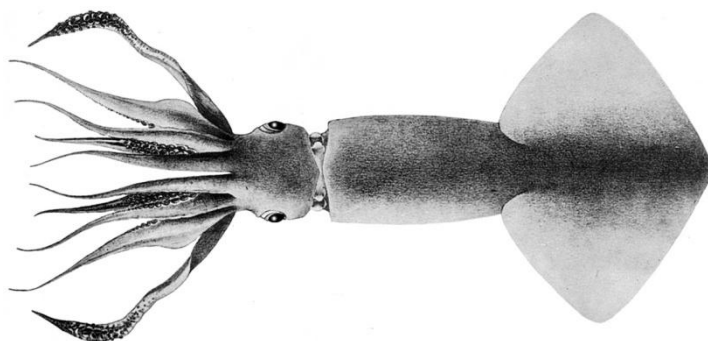


Figure 1. *Dosidicus gigas*, Humboldt or jumbo squid (Orbigny, 1835).

Both the initial appearance in Monterey (USA) and the subsequent spread of strandings appeared to be associated with warm-water anomalies – El Niño in the former case, and events off Baja California (2002) and US Pacific coast (2004-5) in the latter (Weise et al., 2006).

A similar range expansion during this period was also reported in the southern hemisphere (Ibáñez and Cubillos, 2007; Alarcón-Muñoz et al., 2008; Keyl et al., 2008). It is thought that the success of this range expansion and the great environmental plasticity may be associated with the highly migratory nature of this species (Markaida et al., 2005; Gilly et al., 2006b), together with fast growth rates (1.1 mm ML at hatching to >1000 mm ML in adults during a 1-2 year lifespan) (Nigmatullin et al., 2001), a flexible and opportunistic feeding strategy (Markaida, 2006a) and a high potential fecundity, with up to 32 million eggs per female (Nigmatullin and Markaida, 2009).

In addition to large seasonal horizontal migrations, *D. gigas* undergoes diel vertical migrations into mesopelagic depths during day time (Gilly et al., 2006b). At these mesopelagic depths, *D. gigas* encounters the permanent oxygen minimum zone (OMZ) throughout nearly all of its range during the day, and can remain in oxygen levels less than 20 μM (0.5 mL/L or $\sim 10\%$ surface dissolved oxygen) for hours (Stewart et al., 2012a; Trübenbach et al., in press a). *D. gigas* interacts with a variety of predator and prey species during both horizontal and vertical migrations. Along with its ecological role, the Humboldt squid is an economically important species and the target of the world's largest invertebrate fishery (Rodhouse et al., 2001, 2006; Bazzino et al., 2010) with an average catch of >780,000 metric tonnes from 2006-2010 (FAO 2010). More specifically, this species is of great importance to commercial fisheries of Mexico (Ehrhardt et al. 1986; Nevárez-Martínez et al. 2000; Salinas-Zavala et al., 2003; Morales-Bojórquez et al., 2001a, 2010), Peru (e.g. Yamashiro et al., 1997, 1998; Taípe et al., 2001) and Chile (Rocha and Vega, 2003; Acuña et al., 2006; Zúñiga et al., 2008; Liu et al., 2010).

The aim of this chapter is to provide a comprehensive review of the life history biology, horizontal (including range expansions) and vertical movements, feeding ecology, predators, parasites and fisheries (landings, catch per unit effort [CPUE] and biomass) of this oceanic top predator.

2. Life History Biology

2.1. Early Life Stages

Little is known about the spawning and embryonic development of this pelagic squid. *D. gigas* spawns in the relatively inaccessible open sea and, like other ommastrephids, extrudes its eggs in a large and fragile pelagic gelatinous mass. In fact, it was only on June 21st 2006 that the first natural egg mass deposition (2 to 3m in diameter) was observed during a blue-water dive in the Guaymas Basin of the Gulf of California (at 27°7.1'N – 111°16'W) (Staaf et al., 2008). The egg mass was neutrally buoyant at ~16 m depth and at a temperature of ~22°C. With an egg density of 192 to 650 eggs/l, the potential number of eggs in the entire mass ranged from 0.6 to 2 million (Staaf et al., 2008).

Using artificial fertilization techniques, Yatsu et al. (1999) showed that hatching occurs between 6 to 9 days after fertilization at 18°C. Size at hatching varied between 0.9 to 1.3 mm ML and post-hatching growth rate was around 4% ML d⁻¹ at that temperature. More recently, Staaf et al. (2011) showed that temperatures below 15°C and above 25°C do not permit complete *in vitro* development and hatching, and that within this temperature range, development is slower at 15°C (around 10 days and with greater mortalities) than at higher temperatures.

Thus, successful embryonic development likely only occurs in areas of the eastern Pacific where temperature at the pycnocline is within that thermal range. During the late summer and early fall, a pycnocline at 15°C is found within 500 km off the US coast to at least 40 °N (Staaf et al., 2011), potentially providing suitable spawning habitat for adult squid at a considerably shorter distance than that to Baja California, the closest known spawning area (Ramos-Castillejos et al., 2010). In the Gulf of California, the presence of *D. gigas* paralarvae has been reported from San Pedro Mártir and Guaymas basins by Gilly et al. (2006a) with a higher abundance in the summer months (Camarillo-Coop et al., 2011). The distribution of paralarvae seems to reflect the adult distribution as the fishing grounds in the Gulf of California (Figure 2) are located off Santa Rosalia from May–October and Guaymas from November–May (Camarillo-Coop et al., 2011).

In the southern hemisphere, spawning appears to be widespread, but published information about specific spawning habitats is scarce. During a four-year survey conducted in Peruvian waters by Tafur et al. (2001) the spawning apparently took place along the entire coast of Peru, especially in the northern zone between 3°S and 8°S and the central zone between 12°S and 17°S.

As a member of the family Ommastrephidae, *D. gigas* passes through a post-hatching paralarval stage called the rhynchoteuthion. During this stage, the two tentacles are fused into a well-developed proboscis, which is quite thick and much longer than the arms, up to 80% of ML. The separation of the proboscis is thought to begin at 5 to 6 mm ML and to be completed

by about 10 mm ML. No eye or intestinal photophores (light-producing organs) are present in Humboldt squid paralarvae ranging from 0.8 to 6.0mm ML (Yatsu et al., 1999; Ramos-Castillejos et al., 2010). Gilly et al. (2006a) also reported the presence of eye and intestinal photophores in two paralarvae of 8.0mm ML. Yet, Nigmatullin and Dubinina (cited in Nigmatullin et al., 2001) noticed photophores develop in juveniles between 12–15mm ML and 100–140mm ML, which indicates some variability in the ontogenetic timing of these structures.

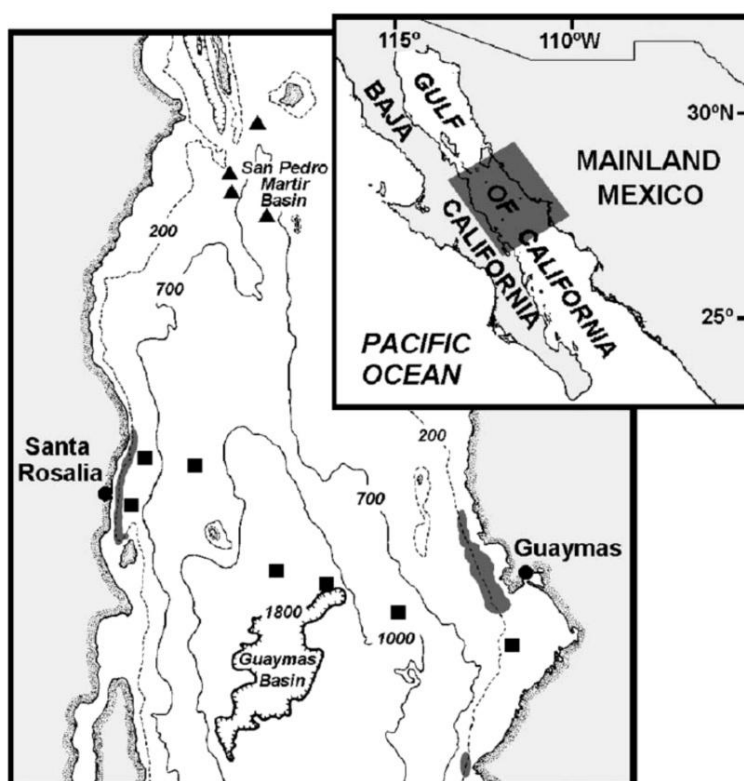


Figure 2. The Guaymas basin in the Gulf of California, showing jumbo squid fishing grounds (in dark gray) off Santa Rosalia (May–October) and off Guaymas (November–May) (from Markaida et al., 2004).

2.2. Age and Growth

The age and growth of *D. gigas* has been investigated using length-frequency distributions (Nesis 1970, 1983; Ehrhardt et al., 1983; Keyl et al., 2011), statolith ageing techniques (Arkhipkin and Murzov 1986; Masuda et al., 1998; Arguelles et al., 2001; Markaida et al., 2004; Mejía-Rebollo et al., 2008; Chen et al., 2011, 2012) and a tag-recapture approach (Markaida et al., 2005). Nesis (1970, 1983) used ML frequency distributions of mature squid to evaluate the population structure of Humboldt squid and identified three potentially distinct groups based on size-at-maturity, namely: i) a group attaining small size (130–340 mm ML) in tropical regions, ii) a medium-sized group (240–600 mm ML) over the

entire distribution range, and iii) a group in higher latitudes of the distribution, in both hemispheres, that matures at “large” size (400–1200 mm ML) (Nigmatullin et al., 2001). Therefore, more than one form can be found in the same area. More recently, Keyl et al. (2008) confirmed that in the Humboldt Current system only small and large groups of size at maturity occur, which also appear to be both spatially and temporally separated (Argüelles et al. 2008). Indeed, the intra-specific population structure of the *D. gigas* is complex, since this species quickly responds to environmental variability driven by El Niño and La Niña events in both the Humboldt Current and California Current Systems, by rapidly changing its biological characteristics, such as somatic and reproduction investment (Bazzino et al., 2007; Markaida, 2006b; Nigmatullin et al., 2001; Taiepet al., 2001; Waluda and Rodhouse, 2006; Argüelles and Tafur 2010).

Statolith growth increments have not yet been validated for *D. gigas*, but assuming a daily increment similar to other ommastrephid squid (Lipinski 1993; Lipinski et al., 1998), several studies have confirmed the high growth rates shown by cohort analysis, and a life span of 1 to 2 years. Arkhipkin and Murzov (1986) were the first to describe the growth of Humboldt squid through the observation of statolith microstructure. They analyzed 113 specimens and estimated ages of between 4 and 4.5 weeks for squid of 9–10 mm ML and 36–37 weeks for mature females of 460–490 mm ML. Masuda et al. (1998) analyzed statoliths of 584 specimens and the age estimates varied between 44 days for a juvenile of 20 mm ML and 338 days for a female of 860 mm ML. Also, Argüelles et al. (2001) assigned ages of 115–200 days to 82 small size squid (100–490 mm ML) and 200–354 days to 52 large squid (520–1100 mm ML). Different models have been used to describe subadult and adult Humboldt squid growth, including the von Bertalanffy using in-size modal-distribution analysis (Ehrhardt et al., 1982, 1986), linear (Masuda et al., 1998), exponential (Arkhipkin and Murzov, 1986; Argüelles et al., 2001) and logistic models (Markaida et al., 2004; Méjia-Rebollo et al., 2008).

Female Humboldt squids are larger than males (Markaida and Sosa-Nishizaki, 2001), and this type of sexual dimorphism is a general pattern in all oegopsid squids. Chen et al. (2012) showed that growth in ML was best described by a linear function for both the sexes, while growth in body weight was best quantified by an exponential function for females and a power curve for males. The maximum absolute daily growth rates and instantaneous growth rate in ML were reached between 181–210 and 151–180 days for females and males, respectively. A growth rate of 1 mm/day was directly demonstrated for large animals in a GC tag-and-recapture study (Markaida et al., 2005). This is the highest growth rate reported for any cephalopod species, and enables this species to reach the reported maximum ML (up to 1200 mm) in its short lifespan (Nigmatullin et al., 2001). Regarding longevity, it has generally been assumed to be no more than 12 to 24 months (Masuda et al., 1998; Argüelles et al., 2001; Nigmatullin et al., 2001). Recent data from the industrial fishery in the Peruvian waters seem to indicate that growth parameters may be more variable, with lifespans ranging from 12 to 32 months. Yet, the only tag-recapture study for *D. gigas* found monthly growth rates between 30 mm and 45 mm (Markaida et al., 2005) that would lead to a lifespan between 17 months and 26 months for an 800 mm specimen.

2.3. Maturation and Fecundity

The Humboldt squid is a monocyclic species (i.e. it dies after a single cycle of gametogenesis and spawning; Rocha et al., 2001) and so its final size is related to its size at maturity. Keyl et al. (2008) argue that, from an energetic point of view, squid maturing at small sizes benefit over the larger ones as they can put less energy in somatic and reproductive tissue before spawning. Also, the potentially higher population turnover rate of the smaller individuals (which is not always true, see previous section) decreases the mean trophic level of the population, allowing it to feed at the more productive lower trophic levels. The authors also suggested that, in the Humboldt Current system, the small size-at-maturity strategy ensures that the population survives during warm periods with low food availability, while the large size-at-maturity strategy allows for maximizing individual fitness during cool periods with abundant prey. Thus, changes in reproductive patterns may allow Humboldt squid to cope with productivity changes in their environment.

Humboldt squid that mature at larger sizes have higher fecundities (Nigmatullin and Markaida, 2009). Nesis (1970, 1983) reported a fecundity range from 100,000 to more than 600,000 eggs for the medium-sized form (350–560 mm ML) of Humboldt squid from South American waters. Yet, this author only counted eggs in the oviducts and maturing vitelline oocytes (diameter ~0.8–1 mm) in the ovary, which underestimates total potential fecundity. In fact, due to the asynchronous character of the Humboldt squid's oocyte development and egg maturation, such an estimate may represent no more than 14% the potential fecundity at any given time. Later, Nigmatullin and Laptikhovsky (1994), counted oocytes with diameter greater than 0.05 mm in female Humboldt squid (150–720 mm ML) collected in 1980–1989 from open waters off Nicaragua, equatorial areas and Peru, which yielded an estimated potential fecundity between 0.3 and 13 million eggs. More recently, Nigmatullin and Markaida (2009) suggested that oocyte development is asynchronous with a predominance (85–90%) of small protoplasmic oocytes 0.1–0.2 mm in diameter for all stages of female maturity. They estimated the average potential fecundity to be 18–21 million oocytes and the maximum to be 32 million oocytes, which is the greatest number estimated for any cephalopod species.

Spawning is extended and intermittent, since a female spawns no less than half of the initial potential fecundity, and the minimal number of spawning activity events (egg batches) is roughly estimated at 8–12. Nonetheless, during this terminal spawning stage, females continue actively feeding and grow between egg-mass laying periods (Nigmatullin and Markaida, 2009).

The reproductive period (based on the percentages of mature females) seems to extend throughout the year in the southern hemisphere but with a pronounced peak spawning between October and January (especially in November) and a second peak in July and August (Tafur and Rabi, 1997; Yamashiro et al., 1998; Tafur et al., 2001; Liu et al., 2010). Clarke and Paliza (2000) also reported the existence of the two spawning periods within a year for *D. gigas* in the southern hemisphere, one of the peaks occurring in the austral autumn (April–May) and the other in the austral spring (October–November). In the northern hemisphere, Ehrhardt et al. (1983) first suggested three spawning peaks. However, some of these percentages were too low to be considered as indicator of spawning peak (31.1%, 30%). In the northern hemisphere, since the 1990s the reproductive studies in the Gulf of California have considered other maturity scales and the most used for this species has been from

Lipinski and Underhill (1995). Markaida and Sosa-Nishizaki (2001) found that a small proportion of mature females were present in almost all months (from November 1995 to June 1997, with the exception of December 1996). Similarly, mature specimens were found in all months in Peruvian waters (Tafur et al., 2010). The reproductive period of Humboldt squid caught outside the northern and central Chilean EEZ (20° to 41°S; between 2006 and 2008) is also year round with a peak in the austral summer from November to January (Liu et al., 2010).

Mature females are rarely found to be unmated (Tafur et al., 2010; but also see Field et al., 2012), but it is not known if a single female can store spermatophores of more than one male, (i.e. how such potential multi-paternity of egg batches influences genetic variability of offspring). Also of interest in the context of genetic variability is that the sex-ratio is not constant and changes considerably from year to year in Peruvian waters. In the 1990s, it was around 3:1 (females:males), decreasing to 2:1 in the 2000s (Tafur et al., 2010).

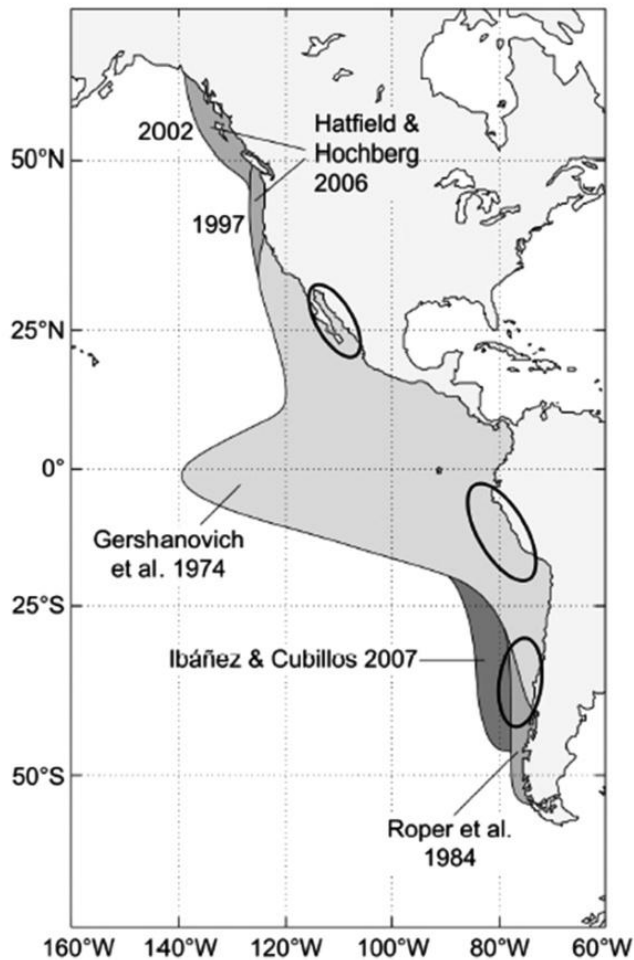


Figure 3. Distribution area of *Dosidicus gigas* indicating an extension of the range (ellipses show the main fishing areas) (from Keyl et al., 2008).

3. Ecology

3.1. Distribution and Genetic Structure

Dosidicus gigas is the most primitive and least oceanic representative of the Ommastrephinae, because it is the only member of this subfamily with a geographical range restricted to just one continental margin (Nigmatullin et al., 2001). Yet, the Humboldt squid exhibits a broad and variable range in the eastern Pacific Ocean and undergoes periodic range extensions. Until the end of the last millennium, the northern and southern limits of Humboldt squid distribution were around 30°N and 40°S, with the highest abundances located in the Gulf of California and in waters off Peru (Nigmatullin et al., 2001).

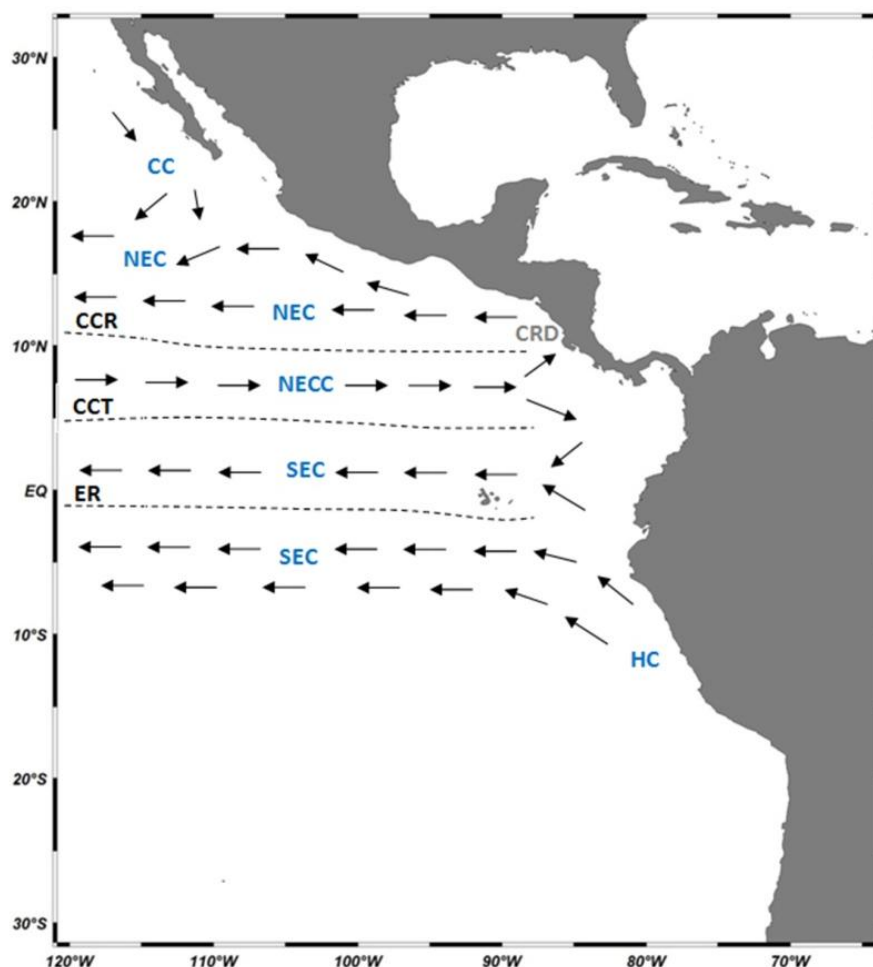


Figure 4. General features of the surface current system of the Eastern Subtropical and Tropical Pacific Ocean (in July-December). Legend: NEC - North Equatorial Current; NECC - North Equatorial Countercurrent; SEC - South Equatorial Current; CC - California Current; HC - Humboldt Current; CCR - Countercurrent Ridge; CCT - Countercurrent Trough; ER - Equatorial Ridge; CRD - Costa Rica Dome.

More recently, the distribution limits shifted to 60°N and 50°S, respectively (Figure 3). In the equatorial region, the distribution may extend as far west as 125° to 140°W (Wormuth, 1998; Jereb and Roper, 2012), but this western boundary is not well documented, particularly in regard to the recent range expansion.

It is noteworthy that there may be genetically separated sub-populations in the two hemispheres (Sandoval-Castellanos et al., 2007; Staaf et al., 2010), probably because the equatorial currents and counter-currents form a natural barrier in the Eastern Tropical Pacific (ETP, Figure 4). Using genetic (RAPD and SSCP) techniques, Sandoval-Castellanos et al. (2007, 2010) found that the level of genetic structure between northern and southern locations is significant enough to support the idea that *D. gigas* is in a process of adaptive radiation (Nigmatullin et al., 2001). Sandoval-Castellanos et al. (2010) also argues that the spatial pattern as well as the very recent divergence (<10,000 years) among northern and southern sub-populations could be explained by oceanographic and biological factors, in particular those affecting ocean productivity. Yet, only mild divergence between south–north populations were observed by Staaf et al. (2010) using the mitochondrial marker NADH dehydrogenase subunit 2. Ibáñez et al. (2011) also found limited evidence of genetic structure in the Humboldt Current system. According to these authors, *D. gigas* consists of a single large population that experienced a dramatic expansion in the Humboldt Current system associated with rise in sea surface temperature and the reorganization of the OMZ in the last 30,000 yr, probably associated with the glacial–interglacial transition.

Physical, biological, and oceanographic factors in the ETP influence the reproductive interchange between potential sub-populations as well as migratory ecology (Anderson and Rodhouse, 2001), which make the dynamics of the genetic differentiation of this species quite complex.

3.2. Horizontal Movements

Although the lack of population structure for *D. gigas* across its large range suggests a high degree of genetic flow and substantial horizontal migration (Staaf et al., 2010), specific migratory pathways in the Pacific Ocean have not yet been demonstrated. Proposed long-distance migrations for *D. gigas* over a large part of its range were originally centered on an equatorial spawning area with migrations into both the southern California Current and the northern Humboldt Current Systems (Nesis, 1983). This model has gone largely untested but is clearly inadequate, because spawning is now known to occur outside of the equatorial core region, both in the Gulf of California (Gilly et al., 2006b; Camarillo-Coop et al., 2011) and the Pacific Ocean off Baja California (Camarillo-Coop et al., 2006; Ramos-Castillejos et al., 2010). In the southern hemisphere, spawning is known to take place off the entire coast of Peru, mainly occurring between 3° and 8°S and 12° and 17°S (Tafur et al., 2001). Recently, a modified version of the Nesis (1983) hypothesis was proposed for *D. gigas* migration in the southern hemisphere between 0 - 20 °S, with a change in this pattern occurring after the 1997-98 El Niño that resulted in an extension of the migration to 40 °S and a large increase in body size (Keyl et al., 2008; Tafur et al., 2010). Long-distance migration is likely to be an important element in the life-history of *D. gigas* and may be associated with differential growth rates and size at full maturity.

Studies based on fishery data and jigging surveys also proposed migrations between the Pacific Ocean and the Gulf of California (Klett, 1982; Ehrhardt et al., 1983). Squid were thought to enter the southern Gulf in winter and reach the Guaymas Basin in the central Gulf by April. In September these squid were proposed to migrate eastward to the Sonora coast and then southwards, eventually back into the Pacific Ocean. Mass migration between the Gulf of California and Pacific Ocean was also proposed to account for the disappearance of commercial quantities of *D. gigas* in the Gulf of California following the strong El Niño of 1997–1998 (Morales-Bojórquez et al., 2001). Although movements into the Pacific Ocean from the Gulf undoubtedly occur, the extent and timing of these movements remains to be determined.

Smaller-scale migrations within the Gulf of California have been documented in the Guaymas Basin (Figure 2), where *D. gigas* has been present year-round since 1994 and supports seasonal fisheries off the Baja California peninsula (Santa Rosalia) in summer/fall and off the Sonora coast (Guaymas) in winter/spring. Seasonal migrations between these areas (~130 km apart) were directly demonstrated with conventional tag-and-recapture methods (Markaida et al., 2005). This migration pattern allows the commercial harvest of large squid year-round in the Guaymas Basin and roughly parallels changes in coastal productivity due to wind-driven upwelling (Roden, 1964) and the location of spawning myctophids (Aceves-Medina et al., 2004), the major dietary item in this region (Markaida et al., 2008). The precise routes of these seasonal movements across the Guaymas Basin are not known, and based on pop-up archival tags (PAT) returns it seems that a highly coordinated migration of many squid following a strict route is unlikely. Squid tagged off Santa Rosalia during November when a migration to Guaymas was expected did not all follow the same course, although there was general tendency to move north and east (Gilly et al., 2006b). Tagging in October revealed movements of the same general magnitude to the southwest into the Carmen Basin, as did springtime tagging at both Santa Rosalia and Guaymas (Gilly et al. 2012). Unfortunately, the numbers of tags deployed in these studies were too small to allow definitive conclusions.

PAT tags have also been used with *D. gigas* in the Pacific Ocean off the Baja California peninsula (Bazzino et al., 2010) and central California, USA (Stewart et al., 2012a). In the former case, tags were deployed near the entrance to Magdalena Bay in June, and a seasonal fishery has developed during the last decade in this highly productive area. This study suggested that squid tended to spend several days foraging in the relatively shallow (100 m) area outside the bay where tags were deployed and then move to deeper offshore waters. Such an onshore-offshore migration has since been documented in the Gulf of California using acoustic sampling (Benoit-Bird, unpublished data) and off the coast of Washington using acoustic tags (Stewart et al., 2012b); it is likely a common behavior of this squid that is known to favour coastal shelf and canyon habitats and in the CCS feed on organisms found in both environments (Field et al., 2012).

Migrations of Humboldt squid in the northeastern Pacific have been documented indirectly in conjunction with scientific sampling of other species, commercial and sport fishing reports and coverage of strandings in the popular media, as well as directly through tagging studies.

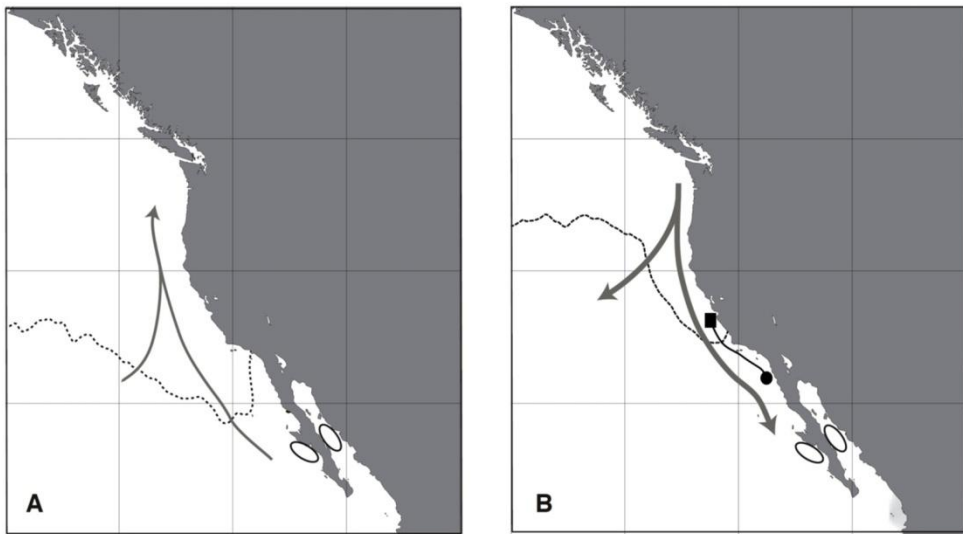


Figure 5. Proposed seasonal migrations of *Dosidicus gigas* in the California Current System (after Field et al., 2012). Gray arrows show the hypothesized migration routes north by smaller, immature squid (A) and south by mature, large squid (B) with potential for offshore movement. Dotted lines show the location of the 15°C thermocline. The area south of this boundary is potentially suitable for spawning, because conditions are thought to be suitable for complete embryonic development and hatching of paralarvae. Documented spawning grounds are shown as ellipses. Black line in B) shows the migration of one squid tagged in autumn with a PAT tag in 2009 (square: deployment location, circle: pop-up location) that traveled horizontally ~40 km/day and up to >50 km/day, covering a net distance of 600 km in 17.5 days (Stewart et al., 2012c).

The indirect methods, along with demographic data from squid sampled throughout the year at different locations, strongly suggest a seasonal migration from southern and central California to shelf areas off the Olympic Peninsula (Washington, USA), Vancouver Island and the Queen Charlotte Islands (Canada) (Field et al., 2012) (Figure 5).

According to this hypothesis, smaller Humboldt squid (<500 mm ML) first appear in central California during late spring or early summer and are then thought to move north to waters off of Washington and British Columbia, where they are abundant (and of larger size) during late summer and early fall.

During late fall and early winter, large squid (> 600 mm ML) are proposed to return on a southward migration, again passing through central California, presumably on their way to spawn in suitable waters to the south or west. Humboldt squid are estimated to swim ~40 km/day horizontally during these migrations (Stewart et al., 2012c). Growth during this putative migration would be consistent with a 1 mm/day increase in mantle length measured in tag-and-recapture studies (Markaida et al., 2005).

3.3. Vertical Movements and Hypoxia

Dosidicus gigas, like other ommastrephid squids, undertakes diel vertical migrations from midwater depths during the day into near-surface waters at night (Roper and Young, 1975, Nakamura, 1991, 1993, Nigmatullin et al., 2001; Gilly et al., 2006b, Stewart et al.,

2012a). Daytime depths throughout its large range in the eastern Pacific are characterized by the presence of a pronounced midwater zone of oxygen-depleted water known as the oxygen minimum zone (OMZ). This major environmental feature results from a combination of oceanic currents delivering oxygen-poor water to depth and midwater microbes aerobically metabolizing sinking organic material, further depleting oxygen to concentrations that can approach zero (Roden, 1964). This sinking organic matter is produced in conjunction with the high surface productivity characteristic of the Humboldt and California Currents and equatorial upwelling zones (Gilly et al., 2013). The upper boundary of the OMZ in the Eastern Pacific is generally defined as the depth where the oxygen concentration is 20 $\mu\text{mol/kg}$, but this depth depends on latitude, ranging from ~ 100 m in the southern Gulf of California to ~ 600 m off British Columbia. Another layer of hypoxic water, with an oxygen concentration of 20-60 $\mu\text{mol/kg}$, occurs above (and below) the OMZ. This area above the OMZ is important ecologically and has been called oxygen limited zone (OLZ) (Stewart et al., 2012a; Gilly et al., 2012, 2013). The lower boundary of the OMZ generally lies at ~ 1200 m regardless of location. Below this depth, oxygen concentration rises again to OLZ-levels because of deep-ocean circulation.

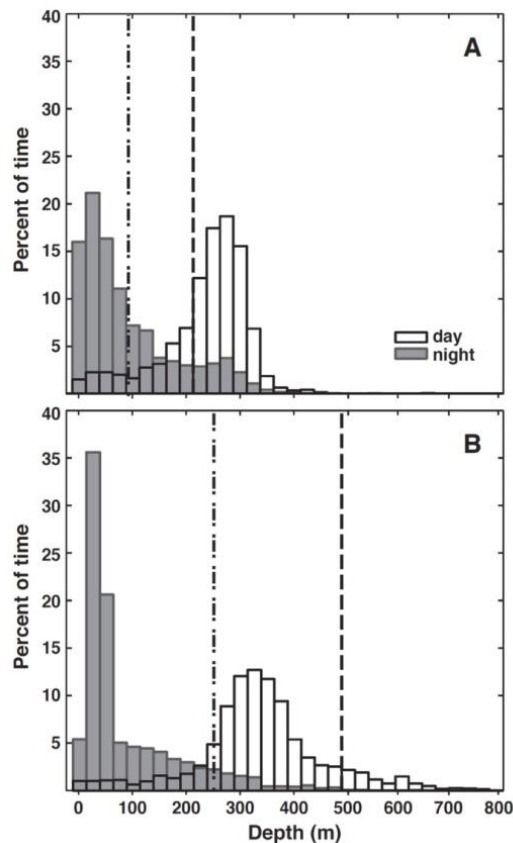


Figure 6. Daytime (unshaded) and nighttime (shaded) depth distributions for *Dosidicus gigas* in A) the Gulf of California, Mexico and B) the northern California Current System off California, USA. Dashed line indicates the upper boundary of the oxygen minimum zone (OMZ) and the dotted-dashed line indicates the upper boundary of the oxygen limited zone (OLZ). Data from Stewart et al. (2012a).

Time-at-depth histograms based on PAT tag data indicate that *D. gigas* spends the vast majority of daytime at depths of several hundred meters, generally in the vicinity of the upper boundary of the OMZ and within the OLZ both in the Gulf of California and the Pacific Ocean (Gilly et al., 2006a; Bazzino et al., 2010; Stewart et al., 2012a; Gilly et al., 2012) (Figure 6). Based on oxygen profiles recorded at the time and place of tagging, *D. gigas* appears to be able to tolerate OMZ conditions ($< 20 \mu\text{mol/kg}$) for > 9 hours (Stewart et al., 2012a), and suppression of aerobic metabolism (Rosa and Seibel, 2008, 2010; Trübenbach et al., 2012 a,b) as well as changes in swimming behavior (Gilly et al., 2012; Trübenbach et al., 2012a) are important mechanisms underlying this capability.

Although squid typically remain deep during daylight hours, vertical movements to near-surface depths often occur, particularly when surface temperatures are cool, either in the California Current System (Stewart et al., 2012a) or seasonally in the Gulf of California (Gilly et al., 2012). Vertical velocities during these forays are highly variable. Nighttime tends to be spent at much shallower depths, generally < 100 m, where *D. gigas* preys on the micronekton that undergoes diel vertical migrations into the epipelagic zone. How long an individual squid remains in near-surface waters at night is highly variable with no apparent predictability. *D. gigas* appears to avoid temperatures higher than 23°C , probably because of a greatly accelerated metabolic rate under such conditions (Rosa and Seibel, 2008, 2010), and temperature probably plays an important role in determining the upper limit of occupancy in the water column (Gilly et al., 2012).

3.4. Diet

By undertaking these extensive diel vertical migrations, *D. gigas* plays a significant role on the vertical energy flow of the Eastern Pacific ecosystems, acting as an important part of the biological pump from the surface to deeperwaters. Diel vertical migrations roughly correspond with those of the acoustic deep-scattering layer (DSL), a community largely composed of mesopelagic micronekton that constitute the staple diet of *D. gigas* (Markaida et al., 2008; Field et al., 2007, 2012). In the Guaymas Basin of the Gulf of California, DSL daytime depths correspond roughly to the upper boundary of the OMZ (Benoit-Bird, pers. comm.), but in the northern California Current System the relationship may be more variable, but a relationship with the DSLs is thought to be important (Tont 1976; Koslow et al. 2011; Stewart et al., 2012a). The main prey species in the diet of Humboldt squid diet are primarily myctophid fishes, in particular *Benthosema panamense*, *Triphoturus mexicanus* (Gulf of California: Markaida and Sosa-Nishizaki, 2003), *Stenobrachius leucopsarus*, *Tarletonbeania crenularis* (northern California Current: Field et al., 2007; 2012), *Symbolophorus evermanni*, *Myctophum aurolaternatum*, *M. nitidulum*, and *Hygophum reinhardtii* (northern Humboldt Current: Shchetinnikov, 1989; Nesis, 1971). Additionally, Humboldt squid prey on DSL invertebrates including squid *Pterygioteuthis giardi*, pelagic red crab *Pleuroncodes planipes*, euphausiids, pteropods (Gulf of California: Markaida and Sosa-Nishizaki, 2003; Markaida, 2006a, Markaida et al., 2008), euphausiids, gonatid squids (northern California Current: Field et al., 2012), and the gonostomatid *Vinciguerria lucetia* (northern Peru Current: Shchetinnikov, 1989; Nesis, 1971; Rosas-Luis et al., 2011). The relative importance of different myctophid species may vary locally; for instance, while the relevance of *S. evermanni* decreases from coastal to open waters in the Humboldt Current, the opposite

scenario occurs for *M. nitidulum*. Also, the importance of *H. reinhardti* increases in southern areas (Shchetinnikov 1986b). In Chilean waters, some biased results induced by a variety of fishing methods were observed, which prevented attaining definite conclusions about the feeding strategy in that geographic area (Ulloa et al., 2006; Ibañez et al., 2008). For instance, in the industrial purse-seine fleet for jackmackerel (*Trachurus murphyi*), the dominant prey was *T. murphyi*, but this was not the case in the industrial trawl fisheries for Patagonian grenadier (*Macruronus magellanicus*) and Chilean hake (*Merluccius gayi*). Although these are likely to be natural prey items, it is uncertain to what extent feeding in the nets contributes towards stomach contents. During the recent poleward incursions in the California Current System, *D. gigas* revealed different foraging behavior although mesopelagics species continued to form the major part of the diet. Occupation of continental shelf environments lead to intensive feeding on other coastal species, including California lizardfish (*Synodus lucioceps*) and red crabs (*Pleuroncodes planipes*) (Bazzino et al., 2010). Further north, off the coast of the US, Humboldt squid were found to prey on groundfish (*Sebastes* spp.), Pacific hake (*Merluccius productus*), northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*) (Field et al., 2007) and salmon (*Oncorhynchus* spp.) (Field et al., 2012). According to Field et al. (2007), groundfish accounted for 40% by reconstructed weight and hake 30%, while mesopelagic fish, though numerically abundant, only accounted for 5%. There are also important dietary changes throughout ontogeny. While micronectonic fry and young squid (1.5-10 cm ML) feed on mesozooplankton, medium size squid (15-33 cm ML) feed mainly on myctophids and large squid (>40 cm ML) feed on myctophids, squids and larger fishes (Shchetinnikov, 1989).

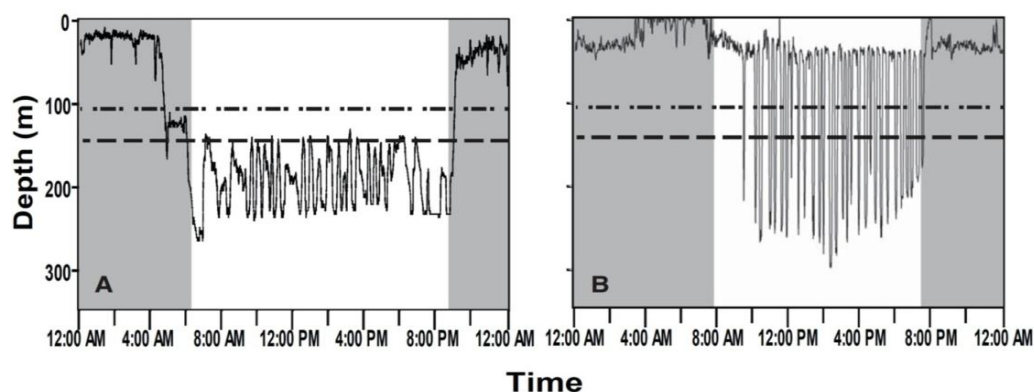


Figure 7. Daytime diving and relationship with hypoxia in the Pacific Ocean off the coast of Baja California for A) Humboldt squid *Dosidicus gigas* (figure adapted from Bazzino et al. 2010) and B) yellowfin tuna *Thunnus albacares* (figure adapted from Schaefer et al. 2007). Dashed line represents the upper boundary of the oxygen minimum zone (OMZ) and dotted-dashed line represents the upper boundary of the oxygen limited zone (OLZ). Oxygen data from cast D of Figure 9 in Bazzino et al. (2010).

3.5. Predators

Adult *D. gigas* appear to be able to tolerate the cold, hypoxic conditions associated with the upper OMZ (Rosa and Seibel, 2008, 2010) for hours (Stewart et al., 2012; Trübenbach et

al. 2012, a,b), which likely provides an advantage for daytime foraging and may also serve as a refuge from predators.

Many other top predators show repetitive diving behavior into the upper boundary of the OMZ during the daytime, including tunas (Childers et al., 2011; Schaefer et al., 2010, 2011), elephant seals (Le Boeuf et al., 2000) and sharks (Weng and Block, 2004; Pardo-Gandarillas et al., 2007; Cabrera-Chavez-Costa et al., 2010). Utilization of this rich daytime foraging ground thus appears to be a common feature of many top pelagic predators (Dewar et al., 2011), some of which prey upon *D. gigas*, but cannot remain within the OMZ for long periods (Figure 7). Other predators of adult *D. gigas* include blue marlins (Abitia-Cardenas et al., 2010), swordfish (Markaida and Hochberg, 2005; Castillo et al., 2007) and sailfish (Arizmendi-Rodriguez et al., 2006).

Although the OMZ may provide some protection from many of these predators, some predators may take advantage of the fact that *D. gigas* moves more slowly in the OMZ (Gilly et al., 2012). Sperm whales in the Gulf of California preferentially hunt at OMZ depths both day and night, presumably because the increased probability of capturing a slow-moving squid outweighs the reduced probability of encounter (Davis et al., 2007; Jaquet and Gendron, 2002). Small and young Humboldt squids are likely preyed on by most small-sized carnivorous fish, (including mahi-mahi/dorado (*Coryphaena hippurus*), snake mackerel (*Gempylus serpens*), yellow-fin tuna (*Thunnus albacares*): Nigmatullin et al., 2001), other squid (e.g. *Sthenoteuthis oulaniensis*), and marine birds (Nigmatullin et al., 2001).

3.6. Parasites

In Equatorial and Peruvian waters (11°N-22°S), the helminth fauna of medium sized *D. gigas* (300-431 mm ML) are mainly composed of larval stages of Didymozoidae, the cestoda *Pelichnibothrium speciosum*, *Phyllobothrium* sp., *Tentacularia coryphaenae*, and the nematodes *Anisakis simplex*, *A. physeteris*, *Porrocaecum* sp., *Contracaecum* sp., and *Spinitectus* sp. (Shukhgalter and Nigmatullin 2001). Larger squid (545-995 mm ML) from a closed area (7-9°S and 83°30'-84°W) also displayed four helminth species, namely *Pelichnibothrium speciosum*, *Tentacularia coryphaenae*, *Anisakis physeteris* and *Porrocaecum* sp. (Nigmatullin et al., 2005). More recently, Pardo-Gandarilla et al. (2009) analyzed the parasitic fauna of 124 Humboldt squids (300-920 mm ML) in the Humboldt Current system off Chile, which was composed of: i) larval cestodes, including *Hepatoxylon trichiuri*, *Tentacularia coryphaenae*, ii) a Tetrphyllidean plerocercoid, *Pelichnibothrium speciosum* and iii) the nematodes *Anisakis* Type I and *Anisakis* Type II. Most of these parasites are transmitted by planktonic crustaceans and small fishes such as myctophids (Nigmatullin et al., 2001). Humboldt squid are considered to be a paratenic host for the larval parasites that infect them, and the definitive hosts are fish, sharks and marine mammals (Shukhgalter and Nigmatullin, 2001), therefore it plays an important role as a trophic link for parasite flow in the Eastern Pacific Ocean.

3.7. Range Expansions

Since 2002, *D. gigas* has displayed an extraordinary extension of its range in the northern hemisphere, beginning near the Mexico - US border (~32 °N) and ending three years later near Tracy Arm in Southeast Alaska (~58 °N), a distance of more than 3,000 km (Gilly et al., 2006b). The Northern limits tended to be reached in late summer and early fall, suggestive of a seasonal migration that reached progressively higher latitudes during this period. Since 2006, the northern limit for the species appears to have withdrawn to the latitude of British Columbia. Most documentation of this phenomenon is derived from reports on strandings and interactions with commercial and sport fishermen and from research trawls targeting other fauna (Cosgrove, 2005; Brodeur et al., 2006; Wing, 2006; Field et al., 2007, 2012). Fishery-independent data for the Monterey Bay area based on submersible sightings (Zeidberg and Robison, 2007) indicate that *D. gigas* suddenly appeared in large numbers after the strong El Niño event of 1997-98 and then disappeared until 2002-03 (Zeidberg and Robison, 2007) when a northward wave of strandings spread up the California coast. Both the initial appearance in Monterey and the subsequent spread of strandings appeared to be associated with warm-water anomalies – El Niño in the former case, and events off Baja California (2002) and US Pacific coast (2004-5) in the latter (Gilly 2005; Weise et al., 2006, Stewart et al., 2012). A similar range expansion during this period was also reported in the southern hemisphere (Ibáñez and Cubillos, 2007; Alarcón-Muñoz et al., 2008; Keyl et al., 2008).

An ability to undergo long-distance migrations is an important factor in such a range expansion, along with a flexible diet, tolerance of temperature change, and fast growth plus high fecundity (Gilly and Markaida, 2007). However, foraging adults pushing their northern limit would have to find suitable spawning habitat within a feasible migration-distance in order maintain any new boundary for the species as whole. A spawning migration from foraging grounds in Canada (50 °N) to known spawning areas off Baja California (27°N: Camarillo-Coop et al., 2006) would cover a distance of ~ 2,500 km. With a lifespan of 1-2 years (Nigmatullin et al., 2001; Markaida et al., 2005), such a migration would be well within the 30-50 km/day migration capability for adult *D. gigas* (Stewart et al., 2012c), but suitable spawning habitat may occur much further north as well (see section 2.1.).

Several factors have been cited that may be acting to drive the range expansion displayed by *D. gigas* during the last decade in the northern hemisphere. Large-scale warming of the sea-surface due to long-term climate change mechanisms has been suggested (Salvadeo et al., 2011), along with removal of competing predators through fishing operations (Zeidberg and Robison, 2007). Shoaling of the OMZ environment has also been proposed (Bograd et al., 2008; Stramma et al., 2012), but this phenomenon is intimately linked to sea-surface warming and increased stratification (Doney et al, 2012; Gilly et al., 2013). In reality all of these factors are likely to play interacting roles that combine in complex ways in different areas across the vast range of *D. gigas*. Nonetheless, the ability of *D. gigas* to make vertical excursions between shallow near-surface waters and the deep OMZ is related to all of them.

Overfishing of large predators, particularly tunas, has been proposed to have reduced levels of predation and competition, thereby aiding *D. gigas* in expanding into new areas (Zeidberg and Robison, 2007), but this hypothesis has been refuted (Watters et al., 2008). At this time, specific theories as to how increased fishing pressure has contributed to the expansion of *D. gigas* do not appear to have been put forward. Which fishery (e.g., yellowfin vs bigeye tuna) was primarily involved, as well as where (e.g., Eastern Tropical Pacific vs.

Gulf of California vs California Current System) and when (e.g., 1960's versus 1980's), remain outstanding questions. Presumably removal of these fishes would primarily affect small, juvenile *D. gigas*, but little is known about the distribution, behavior or life history of these animals, further complicating evaluation of this influence. An alternative hypothesis states that the combined contribution of fisheries and large-scale environmental changes led to the range expansion of *D. gigas* (Keyl et al., 2008). An Ecopath with Ecosim model based on phytoplankton forcing (Tam et al., 2008, Taylor et al., 2008) shows a marked reorganization of the trophic system in the Northern Humboldt Current after the 1997/1998 El Niño. As *D. gigas* is a fast growing, opportunistic predator it occupied feeding "loopholes" of competing species like mackerel and hake after the El Niño "ecosystem reset" (Bakun and Broad, 2003). The fisheries in this scenario are assumed to stabilize the evolving trophic structure with *D. gigas* taking the trophic niche of teleost competitors (Keyl et al., 2008).

Climate change in the Eastern Pacific Ocean would seem to be a more straightforward mechanism to evaluate, particularly in regards to temperature and dissolved oxygen concentration. Many species are constrained physiologically by temperature when undertaking feeding migrations, travelling to the northern extents of their range during the summer and southern limits during the winter in the northern hemisphere (Lam et al., 2008; Pörtner et al., 2008). But *D. gigas* is regularly exposed to great extremes in temperature daily during daily vertical migrations. During typical diving behavior, an individual Humboldt squid can encounter a temperature range of 5-15°C in the California Current System (Stewart et al., 2012a), 10-22°C in the Pacific off Baja California (Bazzino et al., 2010) and at least 7-27°C in the Gulf of California (Gilly et al., 2006b). Thus, it is unlikely that temperature *per se* is directly driving long-distance migration or range expansion as has been demonstrated for other species (e.g. Burrows et al., 2011).

The acoustic DSL is a rich daytime foraging ground targeted by many predators. However, to our knowledge, only *D. gigas* can tolerate the cold, hypoxic conditions that occur at these depths for periods of several hours or more. This ability would allow *D. gigas* to efficiently forage with few competitors in the DSL when it overlaps with the upper OMZ. In addition to simply tolerating the conditions where other predators would be disadvantaged, actively foraging on potentially lethargic animals from below (within the upper OMZ) may confer another benefit for *D. gigas* (Stewart et al., 2012a). Furthermore, although vertical movements exceeding velocities of $\pm 0.3 \text{ ms}^{-1}$ are substantially suppressed under OMZ conditions (Gilly et al., 2012), feeding on myctophids in this habitat is not a high-speed activity (L.D. Zeidberg, pers.comm.). It remains unknown to what extent behaviors necessary to forage in a dense layer of myctophids might be impaired under OMZ conditions.

As the OMZ in the eastern Pacific shoals (Whitney et al., 2007; Bograd et al., 2008; Stramma et al., 2008), myctophids and other mesopelagic micronektonic organisms may be forced to move to shallower and more illuminated daytime depths to maintain a preferred oxygen level. This change could lead to an increased susceptibility to visual predators, and this phenomenon has recently been postulated to account for parallel variations in midwater-oxygen concentration and the number of mesopelagic fish larvae, including myctophids, in the California Current System during the last 60 years (Koslow et al., 2011). The most recent period of oxygen decline (~1997 to present; see Figure 3 of Koslow et al., 2011) corresponds closely to the recent range expansion of *D. gigas*, suggesting that increased predation by Humboldt squid may have been a factor during this time (Stewart et al., 2012a).

A shoaling OMZ and concomitant shifting of the daytime DSL into a depth range closer to the lower photic zone off California could thus lead to a situation analogous to that in the Guaymas Basin in the Gulf of California, an area clearly favored by *D. gigas* (Gilly et al., 2013). Because the upper boundary of the OMZ gets deeper with latitude, this zone would reach a given level of illumination at a later date further to the north as the OMZ shoaled. Thus, the hypothetically important combination of OMZ, DSL and dim illumination that is exploited by *D. gigas* would tend to move northward over time (Gilly et al., 2012). This shifting midwater environmental front may have favored *D. gigas* during its recent range expansion through access to rich foraging grounds that are relatively hostile to competing predators (Stewart et al., 2012a). Given the apparent lack of relevant physiological limitations (pressure, temperature, oxygen), *D. gigas* as a species may continue expanding into the highly productive waters of the California Current system, increasing in both biomass and spatial extent. Any northern range limit is likely to be set by the sustainability of foraging potential within an energetically acceptable distance of suitable spawning grounds. Analogously, the position of the range limit in the southern hemisphere could follow the same reasoning. Since neither of these features would be spatially static, particularly during a time of climate change, the northern limit of this species may continue to be a moving target for some time to come.

4. Fisheries

Humboldt squid support the largest global invertebrate fishery in the world, with the highest annual landings occurring in 2008 (>895,000 metric tonnes) (FAO, 2010). While they are commercially and artisanally fished within the exclusive economic zones (EEZs) of Peru, Chile and Mexico, they are also fished offshore in international waters off Peru, Chile and Central America by Korean, Chinese and Japanese fleets. Humboldt squid have short life cycles (< 2 years), no generational overlap, and are highly migratory, all of which make stock assessments and abundance forecasting difficult. The fisheries have been largely unregulated, and the first quota ever to limit Humboldt squid catch was set by Peru in 2012 at 500,000 tonnes (Murias, 2012).

4.1. Fishing Areas and Methods

Fisheries for *D. gigas* operate mainly in the Gulf of California, Mexico (Nevárez-Martínez et al., 2000; Morales-Bojórquez et al., 2001a) and off the coasts of Central America (e.g. Costa Rica Dome; Ichii et al., 2002; Waluda and Rodhouse, 2005), Peru (Yamashiro et al., 1998; Taipe et al., 2001) and Chile (Rocha and Vega, 2003).

In the Gulf of California, the *D. gigas* fishery began in 1974 with an artisanal fleet mainly composed of small open boats with outboard motors, locally known as pangas, each operated by two fishermen using hand jigs (Nevárez-Martínez et al., 2000). A second type of fleet arose in 1978, when the shrimp trawler fleet switched to squid fishing during the closed season for shrimp fishing. In 1981, this fleet comprised 285 shrimp boats. Between 1983 and 1987, the stock was greatly reduced and the squid fishery disappeared. From 1989 to 1992,

the National Fishery Institute of Mexico conducted exploratory fishing with the participation of 6 Japanese jigging vessels, controlled by Mexican companies, and found significant quantities (see next section) on the western coast of Baja California (Klett, 1996). At the present time, squid are captured artisanally from small open vessels (pangas) that operate for a few hours close to the shore with hand line jigs and lights to attract squid. There are two main production areas: Santa Rosalía and Guaymas. The activity of this fishery extends throughout the year, but occurs mainly between April and September in Santa Rosalía and between October and July in Guaymas (Hernández-Herrera et al., 1998; Morales-Bojórquez et al., 2001). Although the species is also widely distributed in the Mexican Pacific, operating patterns are restricted to the central-northern Gulf of California and on the Pacific side (from Bahía Magdalena to Ensenada) and have a marked seasonality.

In Peru, artisanal fishing is done in wooden boats of 1 to 15 m³ storage capacity. They use hand jigging but other fishing gear such as curtain, purse seine and longlines are occasionally used. Although this squid has been taken as bycatch by artisanal fisheries, since the early 1990s there has been an increase in industrial vessels, largely from East Asia (Japan and Korea), fishing off Peru and Central America, with a resulting increase in squid catches from the eastern Pacific Ocean (Yamashiro et al., 1998; Ichii et al., 2002). The fishing grounds are mainly concentrated off the coast of Peru at 4°S to 10°S; the jigging grounds in the open ocean are located off Peru at 3°S to 18°S and off Central America in high seas waters between 5°N to 10°N, with most fishing taking place in waters deeper than 1000 m (Waluda and Rodhouse, 2005; Waluda et al., 2006). The industrial vessels have between 200 to 1000 m³ of storage capacity operating between 42 and 56 automatic jigging machines (Mariátegui, 2009). A light system consisting of two parallel lines of 160 2kw lamps are used in the fishing operations to attract the squid (Mariátegui, 2009). In common with other jig fisheries for squid, the powerful incandescent light emitted by the jig fishery for *D. gigas* are visible in satellite imagery obtained from the US Defense Meteorological Satellite Programme - Operational Linescan System (DMSP-OLS) (Waluda et al., 2004; Waluda and Rodhouse, 2005, 2006). Although fishing is usually done at night, it can also be done during the day when the abundance is high. The duration of each trip varies between 15 and 40 days depending on the resource availability (Yamashiro et al., 1998).

In the Chilean EEZ catches of Humboldt squid according to the landings given by the National Fisheries Service of Chile (SERNAPESCA) occur mainly in two areas. The most important fishing grounds are situated off the central Chilean (region Biobío, 36° to 38.5°S) closely followed by the northern regions of Coquimbo and Valparaíso (from 29° to 34°S). Whether this distribution results from the actual distribution of Humboldt squid or simply reflects the location of the main fishing ports cannot be clarified from the available data. Nonetheless, these two fishing areas roughly coincide with the latitudinal extent of the main fishing areas of industrial fleets operating in international waters off Chile. Additionally, Japanese, Korean and Chinese industrial jigging exploit Humboldt squid in international waters off South America (Liu et al., 2010a). Chinese and Japanese scientific surveys and data from their respective industrial fishing fleets provide information on fishing activities outside the EEZ of Peru, Chile and Central American countries. Japanese fleets are reported to have operated in the Eastern Tropical Pacific off Costa Rica at least in the late 1990s (Ichii et al., 2002). The first scientific surveys in 2001 off Peru and Costa Rica were followed by first commercial catches outside the Peruvian waters in the fishing area between 5° and 20° S (Chen et al., 2008). Three Chinese scientific surveys off northern and central Chile from 2006

to 2008 (Chen et al., 2010, Liu et al., 2010) accompanied the southwards extent of fishing operations off Chilean waters between 2007 and 2009. DMSP-OLS Satellite imagery shows the extent of the industrial fishery operating in international waters outside the Exclusive Economic Zones (EEZs) of Peru, Chile and Central American, likely to be targeting *D. gigas* (Waluda and Rodhouse 2005) (Figure 8). Further analysis of satellite imagery would provide valuable information on distribution and range expansions and even on abundances if compared with known data of other industrial fisheries on Humboldt squid. Methods for the analysis of nighttime satellite images has been described for instance in Waluda et al. (2002, 2004) and the raw satellite images can be obtained via the National Oceanic and Atmospheric Administration (NOAA) of the USA.

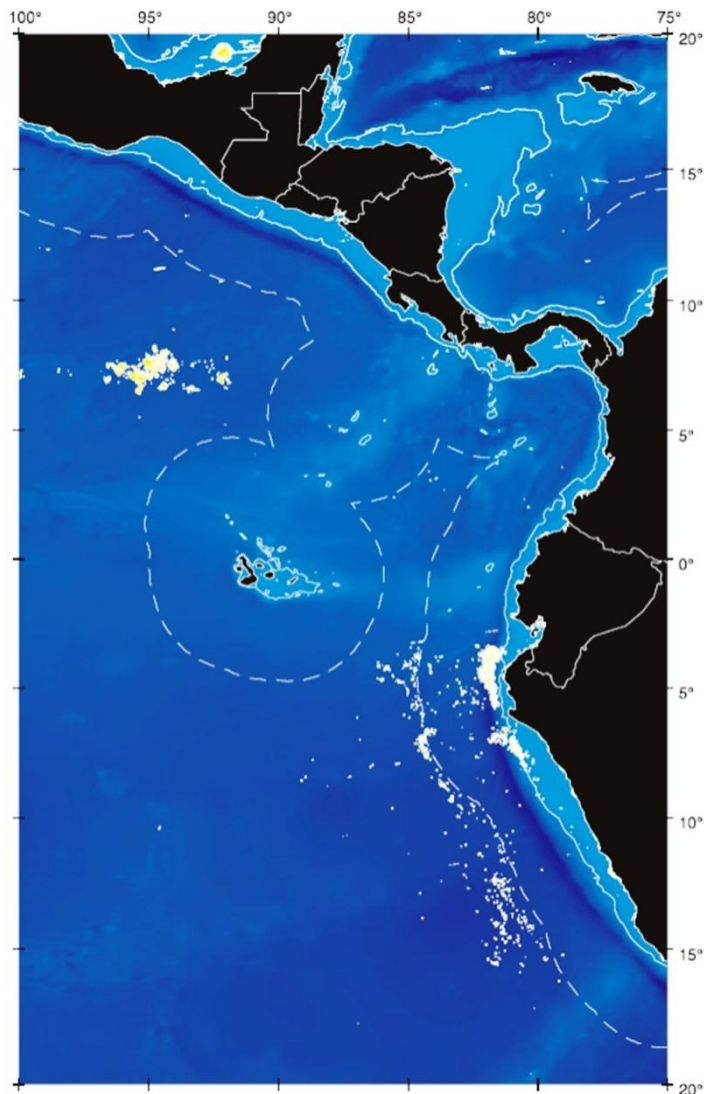


Figure 8. Satellite imagery showing the extent of the industrial fishing in international waters and in the Exclusive Economic Zones (EEZs) of Peru, Chile and Central America, likely to be targeting *D. gigas* (from Waluda and Rodhouse 2005).

4.2. Landings, CPUE and Biomass

The Humboldt squid fishery started in Mexico as a local artisanal activity at the beginning of the 1970s.

The “artisanal period” was characterised by four years of landings of around 2000 tonnes by the artisanal fleet operating (during the summer) from ports in Santa Rosalía and Loreto, Baja California Sur (BCS). After the federal government negotiated access to Asian countries, large companies equipped squid boats with the technology and capacity to process squid on board. This influx of specialised boats began in February 1980 and culminated in November of the same year with landings of 22,464 t (Figure 9). In 1981, the catches declined by one-half to around 11,000 tons, and in 1982 the fishery collapsed (Ehrhardt et al., 1983; Ramirez and Klett, 1985). The fishery took off again in 1994 when Korean and Chinese companies began operating in the ports of Guaymas (Sonora), Santa Rosalía and Loreto (Baja California Sur) and La Reforma (Sinaloa). The landings reached an historical maximum of 117,351 t in 1997, followed closely by those in 2002. In 2010, the total catches were around the 60,000 tons (Figure 9).

The variability in CPUE and stock biomass in the central Gulf of California has not been studied on an annual basis (Hernández-Herrera et al., 1998; Morales-Bojórquez et al., 2001b; Nevárez-Martínez et al., 2000), and therefore the available information does not provide a comparative long-term analysis.

In Peru, between 1964-1971, Humboldt squid was only found as bycatch of coastal trawl and purse seine fisheries, and after this period, the end of which coincided with the major ENSO event in 1972, it was absent or scarce in the landings until 1989 (Benites and Valdivieso, 1986).

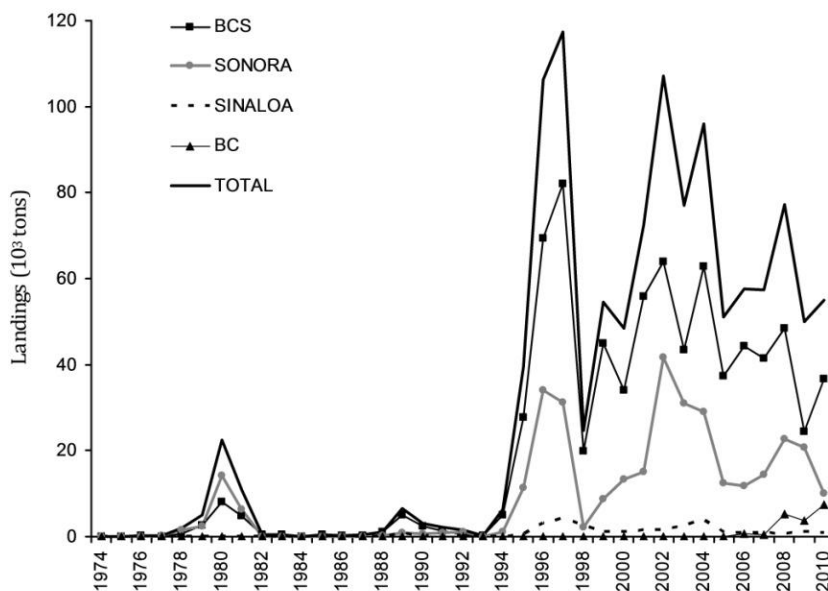


Figure 9. Time series of landings (10^3 tons) of Humboldt squid (*Dosidicus gigas*) in northwestern Mexico. (legend: BCS- Baja California Sur; BC - Baja California) (data from SAGARPA, 2012).

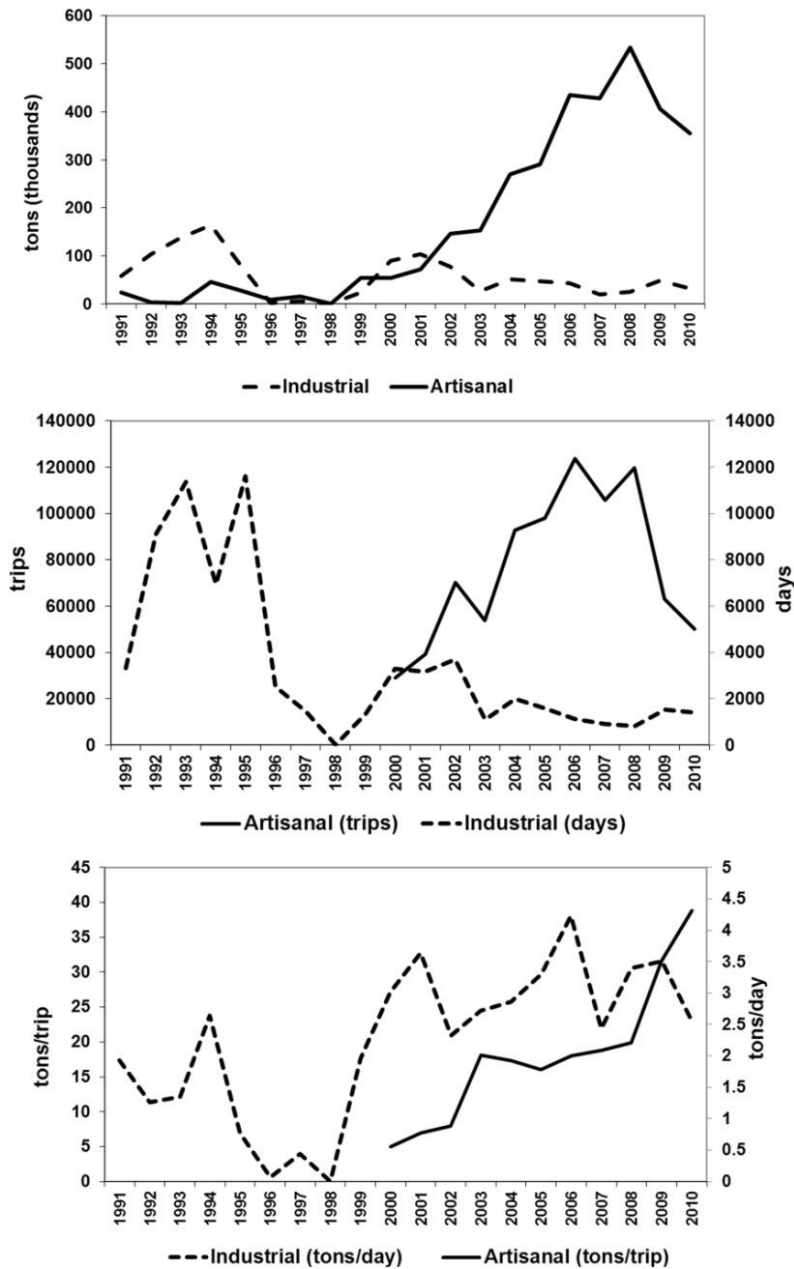


Figure 10. Landings (upper panel), fishing effort and catch per unit effort (CPUE; lower panel) of *Dosidicus gigas* off Peru. Artisanal fleet (black line) and industrial fleet (dotted line) (data from Instituto del Mar del Perú-IMARPE and Ministry of Production-PRODUCE).

The industrial Humboldt squid fishery in Peru began in April 1991 with the participation of Japanese and Korean fleet (within the EEZ under fishing licenses). Annual catches fluctuated between 57,703 and 164,715 tons in the period 1991-1995, in the following years (1996-1998) catches were very low due to oceanographic changes produced by La Niña 1996 and El Niño 1997-98.

Since 1999, there has been a gradual increase in catches, with greater participation of the artisanal fleet and a reduction in the number of industrial-scale jigging vessels. Between 2004 and 2010 annual catches ranged between 340,000 and 560,000 tons, which highlights the participation of the artisanal boats that represented 90% of total catches (Figure 10). It is worth noting that there is a seasonality in landings. At the artisanal level (from 1991-2010), the larger landings occurred in austral summer and autumn and tended to decrease in winter and spring. On the other hand, landings by the industrial fleet shows a reverse trend, with higher landings in winter and spring, because the resource then is more accessible offshore where these vessels operate (Figure 11).

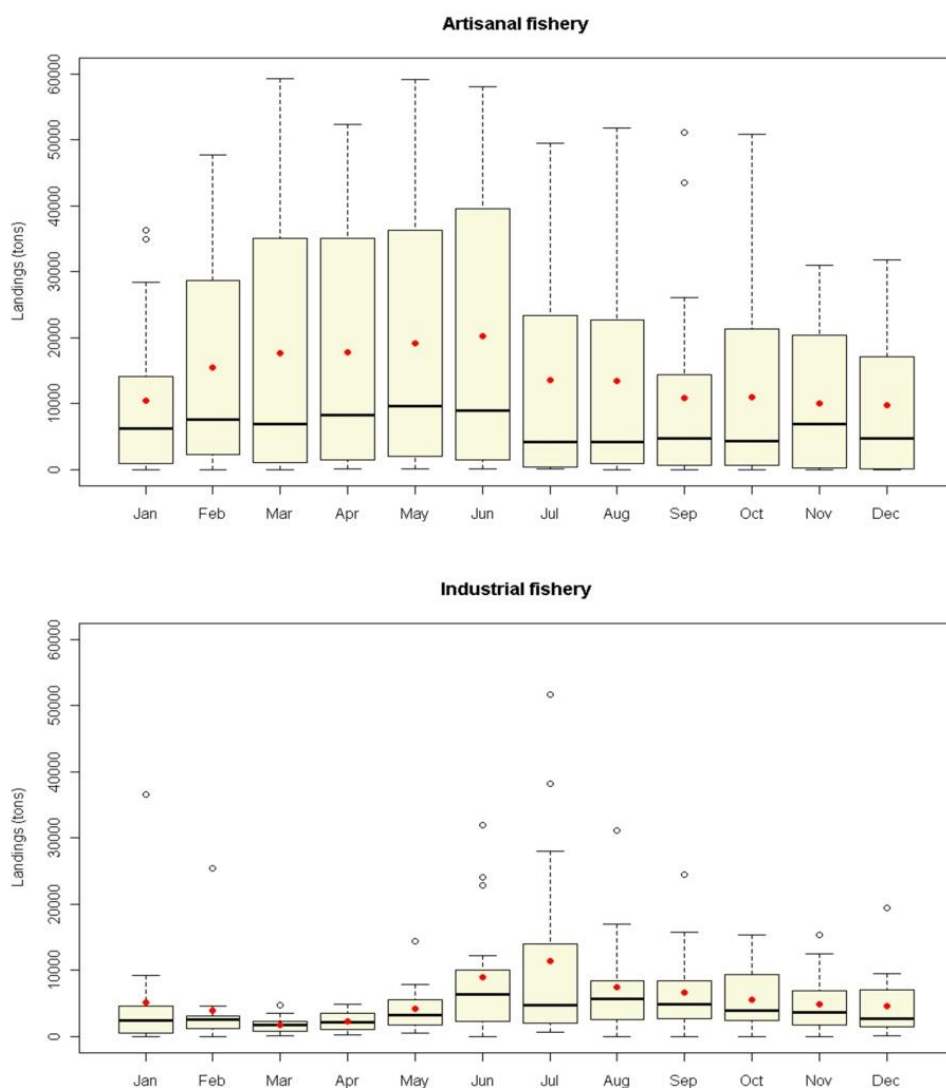


Figure 11. Monthly landings of *Dosidicus gigas* in the artisanal fishery (upper panel) and industrial fishery (lower panel) during 1991-2010 (data from Instituto del Mar del Perú-IMARPE and Ministry of Production-PRODUCE).

Fishing effort of the industrial fleet was higher in 1991-1995 with 31 to 77 jigging vessels with the maximum number in 1993 and 1995. In the following years, the fishing industrial effort was greatly reduced and from 2000 onwards, the artisanal effort increased and peaked in 2006-2008 (Figure 10). CPUE values also showed significant interannual variations, with two periods of high abundance in 1991-1995 and 2000-2010, and an intermediate phase of lower abundance between 1996 and 1998. Since 1999, CPUE increased to values up to 38 tons/day in the industrial fleet and 4 tons/trip in the artisanal fleet in 2006 and 2010 respectively (Figure 10).

In Chilean waters, there are records of landings of *D. gigas* since 1957, but they are sporadic. In other words, *D. gigas* exhibits low-frequency peaks of high abundance and therefore constitutes an ephemeral fishery (Fernández and Vásquez, 1995). Some of periods of high abundance have been reported based on the bycatch of traditional demersal and pelagic fisheries operating in coastal and oceanic waters. Between 1960 and 1972, a maximum of 3021 tons was observed in 1964. Thereafter, less than one ton per year was recorded between 1973 and 1990 (Rocha and Vega, 2003). Between 1991 and 1994, however, the annual catch rose to 9400 tons (in 1992), dropping once again after 1995 to between 1 and 8 tons per year (Figure 12).

The period of higher abundance occurred from 2002 onwards, with a total catch of 296,954 tons in 2005, especially from both the purse seine and bottom trawl fleets off the central-south coast of Chile (Figure 12). Landings in the following years decreased to 56337 tons in 2009 but steeply increased again in 2010 to 200408 tons (SERNAPESCA data). These high abundances were apparently due to: i) the increased reproductive success of this species in Chilean waters, associated with cold oceanographic conditions that occurred in 1999 and 2000, after the El Niño event of 1997–98, or ii) irregular massive invasions into southern peripheries of the central range of the species' distribution (see section 3.2). Since there is no fishery targeting Humboldt squid in Chile, fishing effort data are scarce.

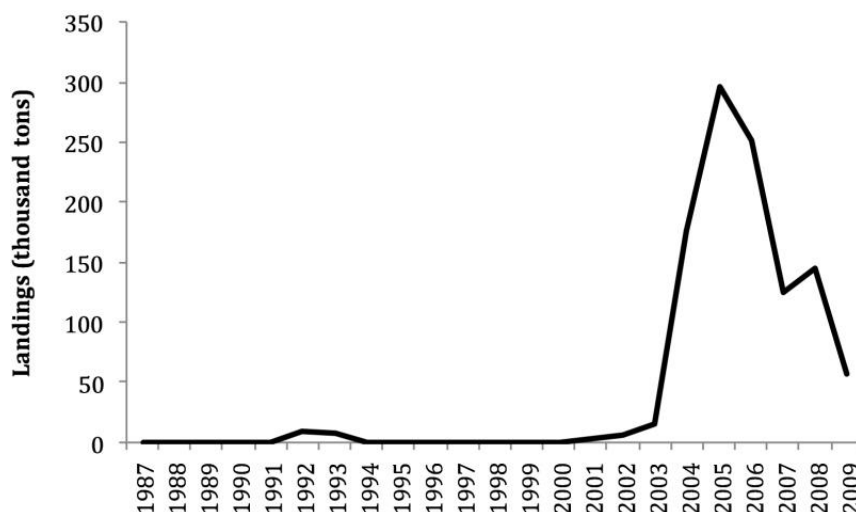


Figure 12. Landings of *Dosidicus gigas* off Chile, between 1987 and 2009 (data from SERNAPESCA, Chile).

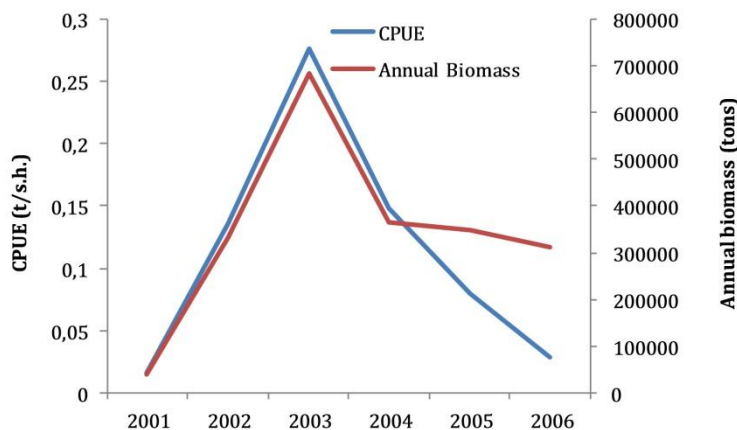


Figure 13. Annual CPUE (tons per sweep hour, t/s.h.) and biomass of Humboldt squid (*Dosidicus gigas*) off central Chile (data from Alarcón-Muñoz et al., 2008).

The highest annual CPUE and calculated biomass values in central Chile were registered in 2003, attaining 0.28 tons per sweep hour and 682,646 tons, respectively (Figure 13; Alarcón-Muñoz et al., 2008).

Available data on catches and CPUE of industrial fisheries on Humboldt squid in international waters is restricted to that of the Chinese fleet. Chinese catches outside the Peruvian EEZ started in 2001 when they already reached nearly 18,000 tons in the first year and increased to over 70,000 tons annually until 2003 in the fishing area between 5° and 20° S. In 2004 the yield was more than 205,000 tons as low catches of *Illex argentine* in SW Atlantic waters forced the Chinese commercial jigging fleet to move to the SE Pacific after April 2004 to target *D. gigas*. The mean catch of 1,728 tons per vessel in that year indicates that nearly 120 vessels were operating in the area. In 2005, landings were again below 80,000 tons. CPUE in 2004 and 2005 were between 5.5 and nearly 9 t per day with highest catch rates at between 9°-10°S and 15°-16°S and from May to December (Chen et al., 2008). During the Chinese scientific surveys off central Chile from 2006 and 2007 CPUE of up to 32 t/d were reached (Liu et al., 2010). No data are available on catches and CPUE in high sea waters outside Chilean EEZ.

4.3. Biomass and Environmental Variability

Environmental variability in the Humboldt Current system is closely related to El Niño-Southern Oscillation (ENSO) events that affect the productivity and availability of fishery resources. The weakening of south easterly Elysian winds allows the advance of warm waters and retreat of the Humboldt Current System, such that pelagic habitat characteristics shift towards the south during El Niño events, the extent and duration of which will depend on the intensity of the anomalies. The opposite effects generally occur during La Niña events. In Peruvian waters, Humboldt squid abundance seems to be strongly affected by high intensity of El Niño events; the CPUE analysis related to the Niño 1+2 anomalies shows highest levels of abundance under moderate thermal anomalies (-2 to +1.5) and decrease substantially to extreme values (Figure 14, see also Waluda et al., 2006).

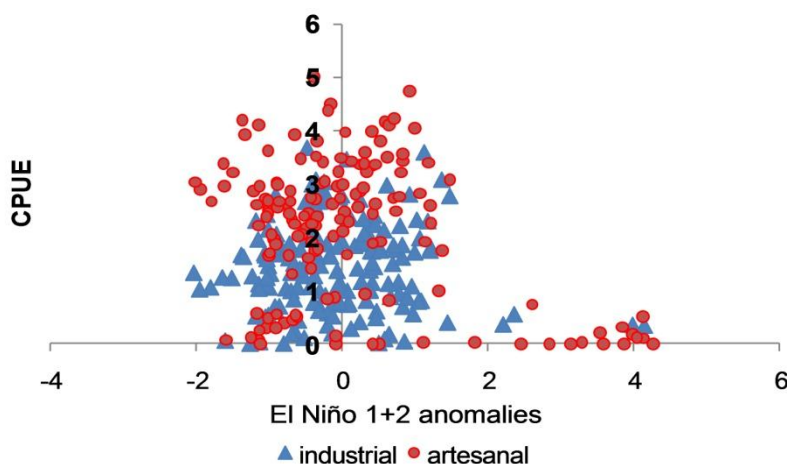


Figure 14. Relationship between CPUE of *Dosidicus gigas* to the El Niño 1+2 anomalies in the artisanal fishery (red color) and industrial fishery (blue color) during 1991-2010 (data from Instituto del Mar del Perú-IMARPE).

The oceanographic characteristics during moderately cold and warm events off the Peruvian coast enhance recruitment and population growth of *D. gigas* due to greater food availability and more rapid development of the early life history stages (Waluda and Rodhouse, 2006). During intense cold or warm events, recruitment is probably affected by lower survival of paralarvae and/or migration of mature adults to other less optimal spawning areas. Such conditions may cause a reduction in the squid abundance off the Peruvian coast, with increasing catches in other parts of the species range, notably around Costa Rica Dome and Gulf of California (Mariátegui et al., 1997; Yamashiro et al., 1998, Taipe et al., 2001; Ichii et al., 2002; Waluda et al., 2006). The intrusion of warmer waters of the California Current System during El Niño events coincided with low recruitment periods, coupled with shift of population structure toward medium size squid (Morales-Bojorquez et al., 2001a; Markaida, 2006b). The recovery in recruitment in Gulf of California began during 2000–2001 and continued to the 2002–2003 (Nevarez-Martinez et al., 2010). The year 2000 was characterized by negative anomalies in sea surface temperature, an indication of a La Niña year that may have triggered the recovery of the subsequent seasons. This pattern appears to show a causal relationship between sea surface temperature and recruitment of *D. gigas* in the Gulf of California (Nevarez-Martinez et al., 2010).

Thus, different processes may be acting on Humboldt squid populations, in the northern and southern hemispheres, under different oceanographic regimes and upwelling conditions, this, and hence the availability of food may be the key factor influencing the aggregation of adult *D. gigas* throughout the species range.

Anderson and Rodhouse (2001) have proposed a working hypothesis that normal conditions and cold La Niña events offshore transport of surface water entrains eggs and paralarvae away from the shelf and westwards towards the central Pacific. Here they become dispersed so the cohort becomes spread over a large area. During warm, El Niño events offshore transport is reduced and eggs and paralarvae are retained near the shelf, especially in Peruvian waters, so that the population attains a high density in the period following an ENSO event.

4.4. Management and Stock Assessment

Managing and forecasting squid fisheries in variable environments constitute a particular challenge because recruitment processes are driven by the environment (Rodhouse, 2001). However, various degrees of management and stock assessments are currently occurring in both hemispheres. Stock assessment in the Humboldt squid fishery is commonly based on the assumption of annual cohorts (Hernandez-Herrera et al., 1998), and therefore the modeling of this resource depends on initial recruitment levels. Management objectives (recruitment and proportional escapement) depend on catchability, which is computed from indices of relative abundance, namely CPUE. One available management strategy uses a constant proportional escapement as a reference point (Beddington et al., 1990; Basson et al., 1996). In Mexico, stock management is based on maintaining a biomass of 40% at the end of each fishing season, and the management strategies to control fishing effort are based on the allocation of fishing licenses or permits. The Mexican National Fisheries Institute bases its estimates and recommendations on the analysis of catch and effort data and information obtained from research cruises. The biomass exploitation has remained above the reference point that gives the status of this fishery as “developing fishery”. Navarez-Martinez et al. (2010) also reported that the fishing mortality (F) and exploitation rate (E) are below 0.5, a level that is considered healthy for an exploited resource. Assessing the impact of fishing through the Thompson-Bell model, it seems that the observed annual fishing mortality ($\bar{F}$) is below the F_{MSY} (associated with maximum sustainable yield, MSY). This is reinforced with the proportional escapement estimate, which is much greater than the biological reference point of 40%. These results indicate that the Humboldt squid is being exploited suboptimally or is underexploited in Mexico.

When present, Humboldt squid are fished recreationally in US and Canadian waters but are not currently targeted by a commercial fishery. However, should a regulated recreational or commercial fishery develop, management could be based on a combination of biological, behavioral, and environmental data along with biomass estimates of the unfished stock—information that often is not available for new fisheries or new management plans.

In Peruvian waters, the Humboldt squid fishery is managed through annual catch quotas, which are determined based on information from the fishery and research cruises. The Humboldt squid stock biomass has been estimated by using acoustics on summer research cruises, and the results show biomasses between 600,000 and 800,000 tons, with a maximum of 1200,000 tons in 2007. The estimated biomass trend indicates that the stock off the Peruvian coast is between 2.5 and 3.0 million tons in the period 2001-2010, and the MSY is about 1.14 million tons (Arguelles, pers. comm.). Management of the Humboldt squid fishery in Chile started in 2012. It includes restricted access, the exclusive use of the catch for human consumption, and a modifiable TAC based on the landings of the last 10 years and actual catches fragmented into industrial (20%) and an artisanal (80%) elements (see webpage SERNAPESCA; <http://www.sernapesca.cl/>).

Managing and forecasting squid fisheries in variable environments constitute a particular challenge because recruitment processes are driven by the environmental variability (Rodhouse, 2001). Fisheries for short-lived species are managed most effectively by effort limitation (Caddy 1983) so there is a need for information about the likely abundance of the next generation prior to recruitment in order to establish fishing effort in advance.

Recruitment variability in several squid species can be explained at least in part by data on environmental data derived from remote sensing imagery (e.g. Waluda et al., 1999, 2006). This is especially critical during the egg and paralarval phases which are most susceptible to environmental conditions. *Dosidicus gigas* inhabits the eastern Pacific coastal coastal upwelling system where the El Niño/Southern Oscillation (ENSO) cycle is one of the best studied ocean/climate systems in the world. Incorporating environmental data into the future management of the fishery has the potential to improve prediction of recruitment and the scientific basis for setting fishing effort prior to the start of exploitation of the next cohort to recruit.

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Chapter VII

***Sthenoteuthis oualaniensis*, Purpleback Flying Squid**

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Abstract

The purpleback flying squid, *Sthenoteuthis oualaniensis*, is a member of the family Ommastrephidae and thought to be the most abundant large squid in the tropical and subtropical waters of the Indo-Pacific region. This chapter describes the life history biology, ecology and fisheries. Because of the relatively low value of *S. oualaniensis*, it is not the main target in the commercial fishery but fishers still take incidental catches of the squid. More research on fisheries and ecology of *S. oualaniensis* are needed in the future.

1. Introduction

Sthenoteuthis oualaniensis, commonly known as the purpleback flying squid, yellow-backed squid, flying squid and purple squid, is a member of the family Ommastrephidae and thought to be the most abundant large squid in the tropical and subtropical waters of the Indo-Pacific region (Dunning, 1998; Young and Hirota, 1998; Figure 1). *S. oualaniensis* occurs from the Red Sea to Australia and from the west coast of Central America to the east coast of Africa, occupying a band from approximately 40° north to approximately 40° south of the

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equator (Roper et al., 1984) (Figure 1). However, its distribution is patchy, being concentrated in areas of high primary productivity (Snyder, 1998).

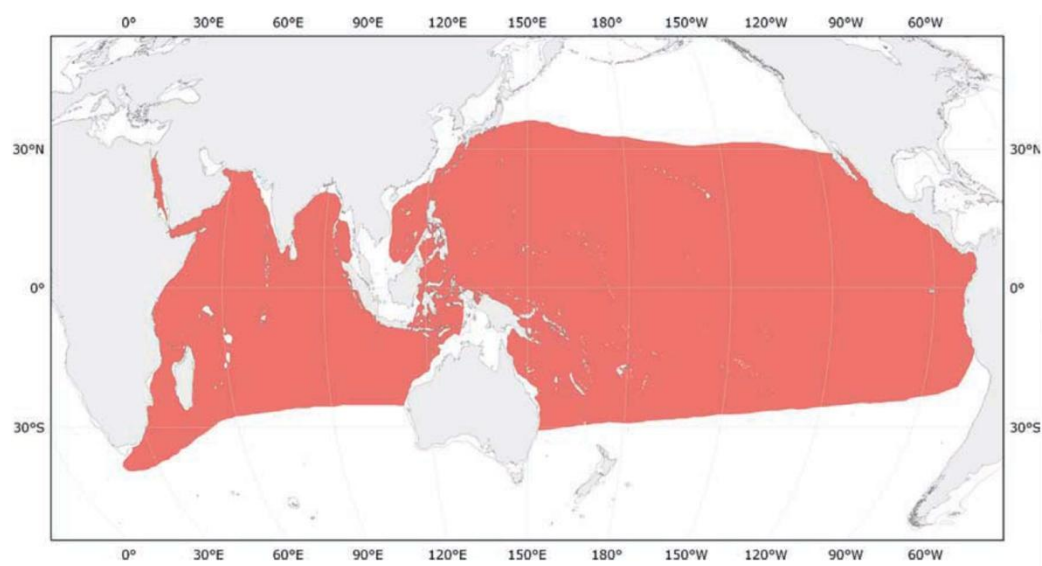


Figure 1. Global distribution of *Sthenoteuthis oualaniensis* (Roper et al., 2010).



Figure 2. Diagnostic features of *Sthenoteuthis oualaniensis*(Chen et al., 2010). A: dorsal view; B: tentacular club; C: arm IV of male hectocotylized.

The mantle of *S. oualaniensis* is very muscular and conical posteriorly, its fins are muscular and broad with the average width of 79% (from 69% to 86%) of mantle length (ML) and the average length of 43% (from 39% to 50%) of ML. Its single fin has an average angle

of 64° (from 61° to 71°). The male squids have wider fins than those of females. The mantle and funnel are fused at locking cartilages. In particular, a large and oval photophoric patch is distributed on the anterodorsal surface of the mantle (Figure 2).

A related species, *Sthenoteuthis pteropus*, the only other member of the genus, replaces *S. oualaniensis* in the Atlantic Ocean. Also, its synonymy is as follows: *Loligo oualaniensis* (Lesson, 1830), *Ommastrephes oceanicus* (Orbigny, 1835-1848), and *Loligo vanicoriensis* (Quoy and Gaimard, 1832).

2. Life History Biology

2.1. Early Stages

In the Pacific Ocean, an egg mass of *S. oualaniensis* has never been seen. But an egg mass, spawned in captivity, by the giant form of *S. oualaniensis* in the Arabian Sea has been reported to have the “typical ommastrephid” appearance (Chesalin and Giragosov, 1993). This means a large spherical, gelatinous egg mass with thousands of eggs distributed throughout the mass. The mature oocytes (eggs) are small, measured as 0.70 x 0.84 mm (Sakurai et al., 1995) or 0.79 x 0.87 mm (Okutani and Tung, 1978) in the oviduct.

The vertical distribution of paralarvae appears to be mostly in the upper 50 m or so of the ocean during both day and night. In Hawaiian waters, 60-70 percent of the paralarvae inhabited the upper 20 m during both day and night with small numbers found in depths of 81-100 m (Young and Hirota, 1998). Most paralarvae are distributed in the upper 70 m in April and the upper 50 m in October, with some captures as deep as at least 150 m in the waters off Oahu, Hawaii (Harman and Young, 1985). Saito and Kubodera (1993) found that the paralarvae mostly inhabited in the upper 40 m in the waters of south of Japan, although they caught paralarvae between 30 m and 60 m over the continental shelf in the East China Sea.

In Hawaiian waters, the paralarvae were present throughout the year but were most abundant in August, less abundant in April and least abundant in October and December (Harman and Young, 1985). Moreover, some seasonal overlaps were observed between the occurrence of paralarvae of *S. oualaniensis* and the related *Ommastrephes bartramii*.

Bigelow (1991) examined growth of paralarvae of *S. oualaniensis* based on the statolith increments of 6 paralarvae and derived a growth curve as $ML = 1.46e^{0.034t}$, where ML is in mm and t is in days. This growth curve indicates that a paralarvae of 4 mm ML is 30 days old.

Little direct evidence is available on the geographical distribution of juveniles although Dunning (1998) was successful in capturing juveniles between 22°S and 39°S where sea surface temperature (SST) was 26.7-20.8°C. According to Okutani and Tung (1978), juveniles are frequently aggregated in inshore waters around oceanic islands such as Hachijo Island, Ogasawara Islands, Seychelles in the Indian Ocean and Guadalupe Island in Mexico.

The vertical distribution of juveniles is also poorly known. Presumably they occupy near-surface waters during the day and night. Small *S. oualaniensis* are found to glide onboard ship during the day (Young and Hirota, 1998). Small *S. oualaniensis* are also observed gliding over the surface of the ocean during the day (Arata, 1954; Young, 1975; Okutani and Tung, 1978) and are commonly found in the stomachs of day feeding birds (Ashmole and Ashmole, 1967). They are also encountered at the surface at night (Young and Hirota, 1998).

The features that mark the end of the juvenile stage in *S. oualaniensis* have never been clearly defined. *S. oualaniensis*, however, has a diagnostic photophore patch on the anterodorsal surface of the mantle. The dorsal photophore patch becomes apparent at approximately 100 mm ML (Kishimoto and Kohno, 1992; Nesis, 1993). The presence of the photophore patch can be taken as a working marker for the end of the juvenile stage and the beginning of the young adult phase.

The hectocotylus develops at about 110 mm ML (Okutani and Tung, 1978). In the study of the age of *S. pteropus* based on statolith by Arkhipkin and Mikheev (1992), they documented a “dark zone” in the statolith characterized by the lower transparency of the statolith and the width of the increments. They found that this ended at about 100-110 days at a ML of about 100 mm which they considered to be the end of the juvenile period for *S. pteropus*.

2.2. Age and Growth

Russian research, reviewed by Nesis (1993), indicates males of *S. oualaniensis* reach 15-17 cm in 6-7 months and are thought to live less than a year. The growth rates, determined by growth marks on statoliths and gladii, of the middle and dwarf forms are nearly the same, but the lifespan is short in the small forms, probably not more than 6 months. Gross growth efficiency (weight of growth divided by the weight of food eaten) is estimated at 10 percent throughout the post-paralarval life.

Yatsu (2000) determined growth curves for both male and female *S. oualaniensis* in the north Pacific based on statolith increments from about 120 mm ML to about 290 mm ML for females and about 185 mm ML for males. His curves are: $ML = 9.9511AGE^{0.634}$ for females and $ML = 29.9AGE^{0.3494}$ for males with ML in mm and AGE in days.

Size for reaching maturity tends to differ between the sexes and have large spatial variability for *S. oualaniensis*. In Hawaiian waters females *S. oualaniensis* start to become mature from 158 mm ML with size at 50% maturity ranging from 166-175 mm ML and 90% maturity at 200 mm ML (maximum size is 335 mm ML). Most males reach maturity by 140 mm ML (maximum size is 210 mm ML) (Young and Hirota, 1998; Suzuki et al., 1986). In northern Australian waters males reached maturity from 160 mm ML and females from 250 mm ML. In the eastern tropical Pacific, Dunning (1998) found males mature over 110 mm ML and females at 180-190 mm ML.

In the northwestern Indian Ocean, the ages of *S. oualaniensis* that were sampled for ageing ranged from 88 to 363 days. All the specimens hatched between January and November 2004, with the majority (57.8%) of hatching occurring from March to May. The oldest squid in the sample grew to the size of 575 mm ML and weighted at 5564 g (Chen et al., 2007). The ML (mm)–weight (g) relationships were estimated (Liu et al., 2009) as: $BW = 40.64 ML^{2.9115}$ for females, and $BW = 45.79 ML^{2.5842}$ for males. The ML–weight equations differed significantly between the sexes. The growth equations of mantle length for spring, summer and autumn populations are, respectively: $ML = 1.4916AGE + 56.458$, $ML = 58.07 \exp[2.7856(1 - e^{-0.05AGE})]$ and $ML = 1.4271AGE + 65.885$.

The growth equations for body weight are: $BW = 99.607 \exp(0.0127AGE)$, $ML = 26.66 \exp[1.741(1 - e^{-0.0012AGE})]$, $BW = 37.221 \exp(0.0176AGE)$ for spring, summer and

autumn populations, respectively. The growth rates in the order from high to low are summer, spring and fall spawning populations (Liu et al., 2009).

2.3. Population Structure

This squid is characterized as having a wide ecological niche and complex intraspecific structure (Nesis, 1993; Zuev et al., 1985). Nesis (1993) described a complex population structure for *S. oualaniensis* that incorporates three major and two minor forms. A giant form that occurs only in the northern Indian Ocean in the region of the Red Sea, Gulf of Aden and Arabian Sea (modal sizes of 400-500 mm ML in the Arabian Sea, maximum size of 650 mm ML), a medium form (modal sizes of 120-150 mm for mature males and 190-250 mm for mature females) that occurs throughout the range of the species and a dwarf form (modal size of 90-100 mm ML for mature males and 90-120 mm ML for mature females, 140-150 mm ML maximum) that occurs in equatorial waters and lacks the dorsal mantle photophore patch characteristic of the species. The medium form may be further divided into two forms based on features of the gladius (double or single lateral axes of the rhachis). One of the two medium forms (single lateral axes of the rhachis) occurs only north of 15°-17°N in the Red Sea, the Gulf of Aden and the Arabian Sea. Complicating this picture is a small form, similar to the medium form but maturing at a smaller size (mode for females is 120-140 mm with a range of 90-160 mm ML) that is nearly the same size as the dwarf form and is found in the Western Indian Ocean and the eastern tropical Pacific. Of the five possible forms, giant, medium with single axis, medium with double axis (the typical *S. oualaniensis*), small and dwarf, the latter three occur in the Pacific Ocean. The dwarf equatorial form is found roughly within 10° latitude of the equator where it co-occurs with the typical *S. oualaniensis*.

The dwarf form has several morphological characters that separate it from the typical *S. oualaniensis* (absence of the dorsal photophore patch, slightly different hectocotylus and slight differences in the spermatophore structure and in the gladius structure [Nesis, 1993]). In Hawaiian waters only the typical *S. oualaniensis* is present. Snyder (1998) suggests that the giant form results from a plastic phenotype in the species. On a more local scale, Okutani and Tung (1978) found *S. oualaniensis* in Taiwanese waters consist of three different seasonal cohorts: a June-spawning group, a September-October spawning group and a February-March spawning group.

In the northwest Indian Ocean, based on the statoliths collected by Chinese squid jigging vessels during 2004 and 2005, three populations, i.e., spring spawning (Jan. to May), summer spawning (Jun. to Aug.) and fall spawning (Sep. to Nov.) can be defined (Liu et al., 2009).

However, the extent of sub-population mixing and genetic isolation is unknown. Several size classes are observed around the Australian waters.

2.4. Maturation and Fecundity

Based on the available evidences, *S. oualaniensis* appears to be a “continuous spawner” (Harman et al., 1989; Young and Hirota, 1998; Rocha et al., 2001) with continuous asynchronous ovulation during the spawning period, and monocyclic maturation of oocytes.

S. oualaniensis tends to spawn over an extended period and its somatic growth decreases during the period of spawning.

Squid are often highly fecund with more than 0.5 million eggs (Trotsenko and Pinchukov, 1994; Zuyev et al., 2002). The batch fecundity for a female of 300 mm ML is 250,000 eggs in the combined oviducts (Harman et al., 1989). The number of oocytes in various stages of development – a proxy of potential fecundity – in a female of 251 mm ML was estimated to be 1,643,000 (Harman et al., 1989). The potential fecundity of the giant form of squid ranged between 2–5 million eggs and the holding capacity of the oviducts was approximately 300,000 eggs (Snyder 1998).

The length of the spawning period and the frequency of spawning episodes during the period are unknown. In addition, geographic variability in the spawning season may exist. Data from Australia suggest that *S. oualaniensis* spawns in austral summer along the continental shelf (Dunning and Brandt, 1985). However, high numbers of paralarvae in the northern Pacific provide support for spring spawning (Chesalin and Zuyev, 2002).

In the northwestern Indian Ocean at 59°-65°E and 5°-25°N, the maturation of females has a clear spatial variation along the latitude (Chen et al., 2007). In the area south to 16°N, most of the squid are in the maturity stages I and II, but the squid of large sizes are in maturity stage III or above. In the area north to 16°N, the squid are generally in the maturity stages III to V. *S. oualaniensis* suggested to spawn all year round based on the ML composition and maturation stage (Chen et al., 2007). This may result from the suitable habitat conditions, i.e., tropical waters with SST being higher than 20°C throughout the year. The peak spawning takes place in March to May (Chesalin, 1994; Chen et al., 2007).

The size at which *S. oualaniensis* become mature differs among different areas. In Hawaiian waters, *S. oualaniensis* females mature between 158 and 205 mm ML with 90 percent mature at 200 mm ML (maximum size is 335 mm ML, 1.6 kg of body weight). Most males become mature by 140 mm ML (maximum size is 210 mm ML; Suzuki et al., 1986; Young and Hirota, 1998). In the north Indian Ocean, however, the females reach maturity between 215 and 560 mm ML with most individuals becoming mature in 420-540 mm ML.

2.5. Statolith and Beak

Liu et al. (2005) studied the morphology and microstructure of statolith of *S. oualaniensis* based on the 114 samples ranging from 142 to 575 mm ML collected during jigging surveys in the northwest Indian Ocean from October to December 2004 and in April 2005. *S. oualaniensis* statolith structure has a great rostrum and small dorsal dome, and its morphological structure is obviously different compared with other squid Families like *Gonatus fabricii*.

The six most important featured parameters including total statolith length (TSL), maximum width (MW), lateral dome length (LDL), ventral dorsal dome length (DLL), rostrum lateral dome length (RLL) and wing length (WL) can be best described by power functions with ML (Liu et al., 2005).

The size of statolith gradually develops with increased ML, while the ratio of each featured parameter to ML slowly decreases and the ratios of FDL, LDL, FRL and WL to TSL almost remain the same, 42%, 57%, 49% and 75%, respectively.

Liu and Chen (2010) studied the beak length and its relationship with ML, body weight as well as age based on 103 beaks and 60 statoliths specimens of *S. oualaniensis* collected during jigging surveys in northwest Indian Ocean from October to December in 2004 and in April of 2005. *S. oualaniensis* beak dimensions are best described by linear functions with mantle length but show positive correlations with exponential equations with body weight. With the squid ontogenetic growth, the size of each part of the beak becomes larger with hood and crest growing faster, but rostrum and wing growing slower. Hood and crest of upper beak grew faster than that of lower beak. Each part dimensions are best described by linear functions with age except the wing of upper beak which fits a power functions better.

3. Ecology

3.1. Distribution and Abundance

S. oualaniensis can be found from the Red Sea to Australia and from the west coast of Central America to the east coast of Africa, occupying a band from approximately 40° north to approximately 40° south of the equator (Roper et al., 1984) (Figure 1). However, it has a patchy distribution, being concentrated in areas of high primary productivity (Nesis, 1977 as cited by Snyder, 1998). Unlike *D. gigas*, it does not form dense aggregations (Nigmatullin et al., 2002).

The biomass of *S. oualaniensis* standing stock in the South China Sea Area III (west of the Philippines) was estimated from jigging surveys at 283,000 metric t (Labe, 2000). Zuev et al. (2002) estimated, based mostly on visual survey methods, the total instantaneous stock size of *S. oualaniensis* at 3-4 million t (1.9-2.4 million tons for the middle-sized form) and an annual production to biomass ratio for adult squids of 8.0-8.5. Nigmatullin et al. (2002) estimated the total stock of *S. oualaniensis* in the world's ocean to be between 8-11 million t. Nigmatullin et al. (2002) described the distribution and biomass of *D. gigas* and *S. oualaniensis* in the eastern South Pacific both outside and inside the EEZ (3° N to 25° S). In the Western equatorial area (1° N to 1° S, 95°- 106°W) the biomass in April to May 1981 was estimated at 940 000 t. This biomass estimates consisted of *S. oualaniensis* (75%) and *D. gigas* (25%). In the Eastern equatorial area (a narrow zone between the boundaries of the EEZ, 3°N to 5°S) the biomass in the same period was estimated at 300 000 t (*D. gigas* 83% and *S. oualaniensis* 17%) (Nigmatullin et al., 2002).

In the north Indian Ocean, the density of *S. oualaniensis* generally ranges from 50 to 75 kg km⁻², and high concentrations are mainly found in the Arabian Sea (Zuevet. al., 1985). Previous studies indicated that *S. oualaniensis* dominated the epipelagial zone of the Arabian Sea both in number and biomass and that the mean biomass was estimated at 4.5 t km⁻² (Chesalin and Zuyev, 2002). The squid density in the area from 20°N to 22°N reached 6.5t km⁻², and the area between 14°N and 15°N even reached up to 12-42 t km⁻² (Nesis, 1993). Based on the Japanese survey, the biomass of *S. oualaniensis* was estimated to be 2 million t (Yatsu, 1997). These studies suggest that the squid could sustain higher exploitation levels (Chen et al., 2007).

3.2. Migration/ Horizontal Movements (and Range Expansion)

3.2.1. Horizontal Migration

S. oualaniensis does not undergo large scale horizontal migrations like *O. bartramii* although the high latitude limits of the population may change seasonally. *S. oualaniensis*, however, does exhibit small-scale areal patterns in the vicinity of islands. Around the Hawaiian Islands large mature females are located on the windward (northeastern) sides of the islands, small immature females are located primarily within 25 km of the leeward (southwestern) sides of the islands and somewhat larger mostly immature females are found mainly further offshore on the leeward sides of the islands (Young and Hirota, 1998). The reason for these patterns is unknown but Young and Hirota (1998) found some differences in feeding patterns between windward and leeward areas. These local patterns and those observed in juveniles (Okutani and Tung, 1978) and in paralarvae (Bower et al., 1999) support a general occurrence for island-related distribution patterns.

The migration patterns of *S. oualaniensis* in the Indian Ocean and eastern Pacific Ocean are unknown. There is no information available on swimming speed for this species.

3.2.2. Vertical Migrations

At night squids are commonly observed from ships in surface waters. Young and Hirota (1998) suggest, based on the near absence of *S. oualaniensis* subadults/adults at night over bottom depths of less than 650 m, that this squid descends to at least 650 m during the day in Hawaiian waters where water temperatures would be around 4°-5°C. Dunning (1998) caught adult *S. oualaniensis* in eastern Australian waters only where bottom depths exceeded 600 m.

It is also found that the vertical distributions change during ontogenesis. Young *S. oualaniensis* (0.5-10 cm ML) usually occur at depths of 15-50 m (Shchetinnikov, 1992). Medium sized *S. oualaniensis* (<15 cm ML) aggregates in shoals of up to 50-60 individuals. *S. oualaniensis* regularly appears in the surface waters at night and actively feed there (Zuev et al., 1985). The shoals become smaller as *S. oualaniensis* grow and larger females (>27 cm) often occur alone. In the Arabian Sea large females are observed between 400- 1100 m depths in the daytime where the oxygen concentration is 0.1-0.2 mg/L (2- 4% of saturation; Shulman et al., 2002) and 50-500 m at night time. In contrast, medium sized females are observed at 50-200 m in the day and at depths of 0-100 m in the night (Bizikov, 1995).

3.3. Feeding Ecology and Behavior

Fast growth rates and high metabolism indicate the requirement of high food intake. It was estimated that adult *S. oualaniensis* require 8-10% of their own body weight as a daily food ration (Shulman et al., 2002).

The feeding spectrum of *S. oualaniensis* was investigated in the southeast Pacific and was found to change considerably with ML. Young feed mainly on amphipods, euphausiids and fish larvae, whereas adults feed primarily on myctophids and secondarily on squid (predominantly *D. gigas*; Shchetinnikov, 1992). Similar prey items were found in similar sized specimens for the Indian Ocean (Nigmatullin et al., 1983). Cannibalism is rarely

observed in the south-eastern Pacific Ocean, however, high rates of cannibalism were recorded in the tropical Pacific and the Indian Oceans (Shchetinnikov, 1992).

In the northwest Indian Ocean, most of the stomachs analyzed had food remains and only 8% were empty (Chen et al., 2007). Preys in the stomachs contained three major groups: fish, cephalopods and crustaceans, representing 56%, 36% and 8% of the stomach contents by weight, respectively. The species remains in the stomachs were identified as *Cypselurus spp* and *S. oualaniensis*, and more than 60% of the stomachs showed the evidence of cannibalism (Chen et al., 2007).

Schetinnikov (1992) found that *S. oualaniensis* fed heavily on crustaceans (up to 50 percent of the volume of the diet) and fish larvae between 40 and 100 mm ML. Between 100 and 150 mm ML the proportion of crustaceans decreased greatly and crustaceans were largely absent at larger sizes. Beyond 150 mm ML myctophids dominated the diet but, as size increased, squids became progressively more important in the diet and by 300 mm ML squids comprised about 40 percent of the diet.

Local variation in the stomach contents of *S. oualaniensis* reported near oceanic islands. Squid captured southwest of Taiwan contained mostly fish, those taken east of Taiwan contained a mixture of fish and squid and around Okinawa they frequently contained crustaceans (Okutani and Tung, 1978). In contrast to a nearly exclusively fish and squid diet in other areas around the Islands (Parry, 2003), mature females captured off the northeastern coast of the island of Hawaii ate mainly crustaceans (Taguchi et al., 1985). Okutani and Tung (1978) found that the stomach weight (relative to body weight) was higher in the first half of the night. Apparently the primary feeding period of subadults and adults follows their arrival in near-surface waters at night.

In Hawaiian waters, Parry (2003) reported that fish and squid comprised virtually the entire diet with fish being more abundant than squid. Stomach contents were analyzed by identifying fish otoliths and squid beaks contained in the stomachs. Among squids, enoploteuthids comprised 17 percent of the diet.

3.4. Predators

The distribution of *S. oualaniensis* overlaps with some of its larger close relatives in the same subfamily (Ommastrephinae), *O. bartramii* at the high latitudinal end of *S. oualaniensis*'s distribution and *D. gigas* in the tropical Eastern Pacific. Schetinnikov (1992) in examining the feeding habits of *S. oualaniensis* in the southeastern Pacific found that large *S. oualaniensis* would consume other species of squid up to 40 percent of its own ML and, in one region studied, fed heavily on young *D. gigas*. This predator/prey relationship suggests that, where their distributions overlap, adult *O. bartramii* and *D. gigas* could be important predators on *S. oualaniensis*. Parry (2003) found no evidence for prey/predator interaction between the two species even though he commonly caught both species at the same site. His study dealt almost exclusively with mature *O. bartramii* and possible interactions between paralarvae and juveniles of both species are unknown, although their primary periods of spawning in Hawaiian waters appear to be somewhat out of phase seasonally and spatially.

Previous studies indicate the presence of *S. oualaniensis* in the stomachs of various predators. *S. oualaniensis* are prey to blue marlin, sooty tern, brown noddy, skipjack and yellowfin and probably bigeye tuna, wahoo and scalloped hammerhead shark (Young, 1975).

S. oualaniensis is also a large proponent of the tropical oceanic seabird *Phaethon rubricauda* diet (Corre et al., 2003) and a primary prey in the diet of some sperm whales (Wang et al., 2002). *S. oualaniensis* made up 0.5 percent of the food items in the stomach and 8.6 percent of the weight (fifth most important) of prey of *Stenella attenuata* near Taiwan provinces (Wanget al., 2003) with the average size of *S. oualaniensis* being 210 mm ML. *S. oualaniensis* comprised 11.5 percent by weight of the diet of the dolphinfish, *Coryphaena hippurus* in the eastern tropical Pacific (Olson and Galvan-Magana, 2002). Off Baja California, *S. oualaniensis* dominated the food of the swordfish in four of eight studies (Markaida and Sosa-Nishizaki, 1998); *S. oualaniensis* made up 26 percent by weight of the diet of the pigmy sperm whales (*Kogia breviceps*) and 2.2 percent (by weight) of the diet of the dwarf sperm whales (*Kogia sima*) off Taiwan (Wanget al., 2002). Ashmole and Ashmole (1967) found *S. oualaniensis* in 34-97 percent of the birds examined at the Christmas Island (Central Equatorial Pacific). Harrison et al. (1983) also found juvenile ommastrephid squid (frequently identified as *S. oualaniensis*) a common item in the diet of seabirds in the Northwest Hawaiian Islands but somewhat less so than at Christmas Island. Wormuth (1976) reported that the snake mackerel, *Gempylus serpens*, is also one of the major predators.

3.5. Parasites

Not known.

4. Fisheries

4.1. Stock Definition and Fishing Areas

S. oualaniensis is commercially fished off Okinawa (in the Ryukyu chain), Taiwan and Hawaii. Fishing grounds existed on the southwestern coasts of Taiwan and beyond the 200 m bottom isobath of the Ryukyu chain (Okutani and Tung, 1978). The fishing season in Taiwan is from March to November with a peak in May-August. Fishing was most productive at SSTs of 26°-28 ° C. The annual landings of squid and cuttlefish in Taiwan provinces and Okinawa from 1947-1969 were averaged 325 tons with 70 percent being *S. oualaniensis* (Okutani and Tung, 1978). The *S. oualaniensis* catch is used for tuna bait and for human consumption (Okutani and Tung, 1978). However, this fishery is not considered valuable because the squid has low values for human consumption relative to other squids as the result of its toughness. In Hawaii the fishery began with immigrants from Okinawa that fished off Hilo at night in small boats with handlines. However, it soon became apparent that they could also catch tuna and tuna quickly became the target of the fishery with squid being used as bait for the tuna or as incidental catch (Yuen, 1979). This night time handline fishery became known as the ika-shibi (squid-tuna) fishery. Between 1973 and 1975 the annual squid catch varied between 0.5 and 5.0 tons (Yuen, 1979). Between 1976 and 1992 the annual squid landings in Hawaii varied from about 1-12 tons with large year-to-year fluctuations and no clear trends.

Many studies of *S. oualaniensis* have been carried out by Russia, Japan and China in the northwest Indian Ocean, and areas with high squid density are identified. During 2003 to 2005, the total catch from Chinese squid jigging fleets attained 5000 t in the northwest Indian Ocean. Because *O. bartramii* in the north Pacific, *D.gigas* in the southeastern Pacific, and *Illex argentinus* in the southwest Atlantic are fully exploited, and the relatively low values of *S. oualaniensis* do not make *S. oualaniensis* the main target of the commercial fishery, fishers still take incidental catches of the squid.

4.2. Fishing Methods

Fishing occurs predominantly by automated jigging using night lights to attract the squid. Chen et al. (2007) reported that there was a high drop-off rate of *S. oualaniensis* in the jigging fishery in the northwest Indian Ocean. Tian et al. (2004) reported that the average drop-off rate was higher than 45% for machine jiggers, but only 7-12% for hand jiggers when using 2 rows of 1.17 mm diameter jigger.

The breaking strength of tentacles was considered as one of main reasons leading to the high drop-off rate of squid, because it can only support 1.06 times of its weight and is as big as 0.367 times of the arm's breaking strength (Chen et al., 2005b).

4.3. Landings and CPUE

There appears to be no directed fishing for this species at present in the Pacific and Indian Oceans. The information on the landings of *S. oualaniensis* is not collected by the FAO.

4.4. Recruitment and Environmental Variability

There is little information on the relationship between the recruitment and environmental variability. Studies on the distribution of fishing grounds with respect to environmental factors have been carried out. Previous studies suggest that fishing grounds of squid were closely related to marine environmental variables such as SST, sea surface height (SSH), wind, chlorophyll-a and zooplankton (Chen and Shao, 2006). The optimum SST on the fishing ground was found to be 27-28°C during September and November, and 26-27°C from December to March in the following year. Most high-yield fishing grounds were distributed in the waters near sea surface height anomalies $SSHA \leq 0$, and the optimal range of salinity in the surface water was from 35.5 to 36.5 (Chen and Shao, 2006; Tian et al., 2006; Yang et al., 2006). On the fishing grounds of high daily catch (over 5 t), we found that the zooplankton mainly consisted of Chaetognatha (average biomass was 9.18mg/m³), Copepoda (2.32mg/m³) and Mysidacea (1.38 mg/m³), and they were present in 86% of all fishing stations (Qian et al., 2006). These three species were also found in the stomachs of squid. Thus they are critical in the formation of fishing ground, and can be considered as indicator species for a squid fishing ground (Qian et al., 2006).

4.5. Management and Stock Assessment

There are currently no known management measures in place for this species in the Pacific and Indian Oceans. Also, there is no information available on estimates of relevant biomass-based and fishing mortality based biological reference points. No harvest control rule and management strategy evaluation have been done.

4.6. Interactions between Fisheries and Higher Trophic Level Predators

Squid jigging is assumed to be a selective and low impact fishing method. The extent of the adverse impacts on the ecosystem from squid fishing is unknown. However, as with any large extraction of resources from the system, changes in community structure are likely. The loss of fishing gear from squid fisheries may also have an adverse effect on the ecosystem. There is no information available on interactions between fisheries and high trophic predators.

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Chapter VIII

***Todarodes sagittatus*, European Flying Squid**

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Abstract

European flying squid, *Todarodes sagittatus* occurs in the Eastern Atlantic Ocean from Iceland, the Barents and Kara Seas southward to Guinea, and westward to the Mid-Atlantic Ridge.

It is a nerito-oceanic species inhabiting mostly slope waters from surface down to >1000 m but also occurs on the shelf and in the open ocean. There are at least three populations – a migratory Northeast Atlantic population that reproduces at the mid-Atlantic ridge and forages as far north as off Iceland and Norway, and resident Mediterranean and Northwest African populations. Spawning takes place on the continental slope and around seamounts with peak in cold season. It is intermittent, females produce from 200,000 to >2,000,000 eggs of 1.1-1.2 mm. Juveniles disperse in surface waters carrying out diel vertical migrations. As they grow and mature, the animals switch to demersal life style gradually moving deeper down the slope. The species has an annual life cycle with some animals in northern waters living slightly more than one year.

It is an omnivorous predator and its feeding spectra mirror the micro- and mesonekton composition, diversity, and abundance in pelagic waters.

Generally the squid feeds on fishes, crustaceans and cephalopods in decreasing order of importance. *T.sagittatus* is preyed upon by a variety of cetaceans, seabirds, elasmobranchs and teleost fishes, the most important predators are swordfish and pilot whales. It is an important paratenic host for anisakid nematodes with intensity of infestation reaching 20-75%.

T. sagittatus is taken as bycatch throughout the species range with no major fishing areas existing nowadays, but it has occasionally occurred in Norway and off Northwest

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Africa in sufficiently large numbers to support a target fishery yielding 10,000-20,000 t per annum. Stocks were not assessed though its annual consumption by predators might be roughly estimated as 2-3 million t.

1. Introduction

European flying squid, *Todarodes sagittatus* (Lamarck, 1799) (Figure 1) was the first ommastrephid known to science (Wormuth, 1998). The holotype is lost. In his description J.B. Lamarck mentioned two varieties of the squid and that the species is distributed and fished along the shores of both Europe and America (Figure 2). The second, small sized form that he was tempted to consider as another species likely was *Illex coindetii*. In 1839 A. D'Orbigny redescribed the holotype as *Ommastrephes sagittatus* and was the first to provide unambiguous diagnosis of the species (Ferussac and D'Orbigny, 1834-1848; Pfeffer, 1912). In the same year J.B. Verany (1839) described *I. coindetii*, separating it from "*Loligo sagittata*". Then M. Philippi established that the two squids have different tentacular club morphology (Philippi, 1844 in Verany, 1851) and the European Flying squid was eventually recognised as a separate species.



Figure 1. *Todarodes sagittatus* from the Northwest African population (ML 290 mm Photo taken by Dr. Oddgeir Alvheim onboard R/V Dr. Fridjorf Nansen in 2000). Courtesy Dr. Hassan Moustahfid (Encyclopedia of Life (EOL) project).

T. sagittatus occurs in the Eastern Atlantic Ocean from the Barents and Kara Seas southward to Guinea (10°45 N – Nigmatullin et al., 1998), and westward its range extends to the mid-Atlantic Ridge and Iceland. It is common as well in the North Sea and in the Mediterranean Sea (Figure 3). The distribution of the species is related to the eastern boundary current system of the North Atlantic and adjacent waters. Such systems are characterised by regions of major coastal upwelling that support high primary productivity, which in turn provide squid populations with enriched feeding conditions (Rodhouse, 2008). The reproductive part of the species range in the Atlantic occupies the hub of the eastern boundary system and includes waters of the Azores Current, the Portugal Current system, and the Canary Current. Squid distribution extends northward into the North Atlantic Drift

Current, waters of the North Sea, and to the Norwegian and North Cape currents that all serve as foraging areas. The functional structure of the species range in the Mediterranean Sea is not clear; probably the species reproduces and forages over the entire water body. The southern part the range of *T. sagittatus* extends into waters of the North equatorial counter current (CIMAS, 2008).

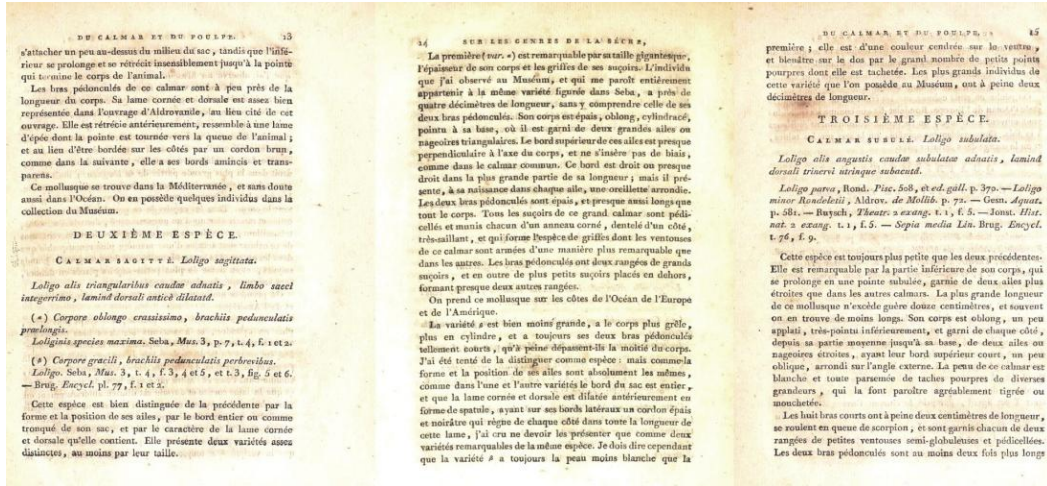


Figure 2. Original description of *T. sagittatus* by J. B. Lamarck.

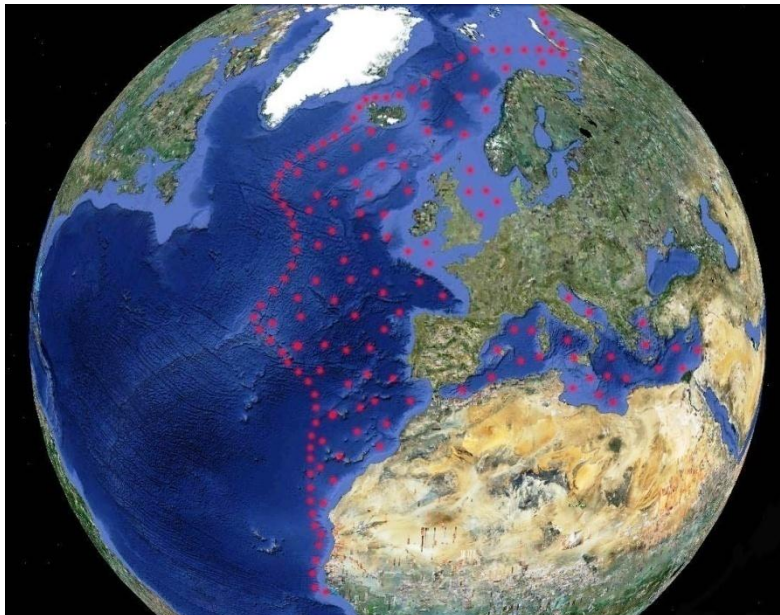


Figure 3. The species range of *T. sagittatus* (background picture downloaded from (<http://earth.google.co.uk>)).

The squid occurs both in pelagic and near bottom layers over the shelf and continental slope down to the depth of ~1,000 m and was captured above 4,595 m depth (Roper et al.,

2010). It is a large nektonic predator attaining > 600 mm ML and consumes a variety of prey: crustaceans, cephalopods and fish.

T. sagittatus is a commercial species that during explosions of abundance can be very important both as a fishery target and as a predator heavily impacting established food webs. Traditionally it was used in Britain, Madeira, Norway and the Mediterranean Sea for bait in longline fisheries, as well as for meal and oil production, and more recently (since the 1970s) – for human consumption (Wiborg, 1978; Arnold, 1979). Before, the species was considered to be inedible because its flesh was supposed to be “hard, skin-like, bitter and unhealthy”. However, this was due to smaller specimens being sold to inexperienced customers, which provoked its prohibition in some markets in the XIX century (Verany, 1851).

A high variability of its stock abundance prevented the development of large-scale stable fisheries across the species range. Specialised fisheries are more or less of artisanal scale, and only in some years of high abundance it may be taken in numbers that represent an adequate target for factory trawlers.

T. sagittatus plays an important role in trophic webs of the shelf and oceanic nekton both as a predator and as prey. It is a part of several levels of the trophic pyramid transferring energy from II-III order consumers to IV-VI order consumers (Nigmatullin, 2004).

2. Life History Biology

2.1. Early Stages

Egg masses and embryonic development are not known (Roper et al., 2010). Presumably eggs are embedded in a gelatinous spherical mass that floats in subsurface waters of the thermocline, as in other ommastrephids (Laptikhovsky and Murzov, 1999; O'Shea et al., 2004). Because the squid eggs are of 1.1 -1.2 mm in diameter (see below) and temperatures of embryonic development probably range between 8 and 15°C, the duration of embryogenesis can be estimated from the equation of Laptikhovsky (1999) as 0.5-1.5 months. Early stages of the species are not described (Wormuth et al., 1992) although they are known around seamounts of the mid – Atlantic ridge from the Azores to 45°N. Paralarvae of 3-10 mm ML aged 20-60 days were collected in this area in December in the upper 50-100 m layer (temperature 8-12°C) (Sennikov et al., 1986).

2.2. Age and Growth

2.2.1. Maximum Size and Age

It is a large-sized nektonic species in which females are larger than males, as in other ommastrephids. The maximum reported size was 750 mm mantle length (ML) and 15 kg body weight (BW) for an unsexed specimen, probably a female (Jaeckel, 1958 in Wiborg, 1972), and 640 mm ML for a male, both caught in North Atlantic waters. Total length is up to 1.5 m (Clarke, 1966).

Maximum sizes historically recorded in the warmer Mediterranean Sea were similar to those in the North Atlantic: 1,655 mm total length, 15 kg BW (Verany, 1851). Recent reports,

in spite of intensive sampling, indicate lower values - 600 mm (6,700 g) and 385 mm (2,600 g) for a female and male respectively (Cuccu et al., 2005). In tropical waters off the Saharan bank squid are even smaller: females and males grow to 350 mm ML (980 g) and 280 mm ML (560 g) maximum respectively (Nigmatullin et al., 1998).

The only reliable way of estimating squid age is counting statolith growth rings (Figure 4). Using this method the maximum squid age was estimated as 409 days in the Northeast Atlantic, with the largest studied mature female (500 mm ML, 3,620 g BW) being 340 days old (Shimko, 1984; Lordan et al., 2001).

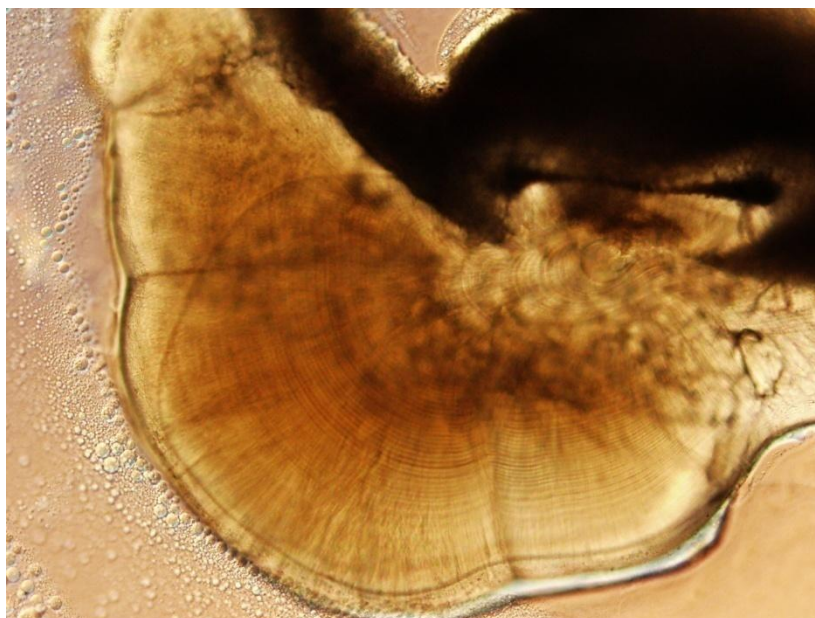


Figure 4. Growth rings on a statolith of *T.sagittatus* (photo by A.Arhipkin).

In the Mediterranean Sea the maximum recorded female age was 354 days (411 mm ML), and that of male – 314 days (282 mm ML) (Quetglas and Morales –Nin, 2004).

In the waters off Northwest Africa the oldest mature unmated female (319 mm ML, age 262 d) was about a month older than the oldest mature male (201 mm ML, age 231 d); the largest specimen – a female of 345 mm ML was 260 days old. However, no spawning or spent squids were aged there, so maximum age might be higher (Arhipkin et al., 1999; Moustahfid, 2002).

This indicates an annual life cycle of the species with some animals in northern waters living slightly more than one year because of natural plasticity in the life cycles of squids (Boyle and Rodhouse, 2005).

2.2.2. Regional Differences in Growth Rates

Two studies in the Northeast Atlantic, 20 years apart, revealed that mean growth rates of females between 150 and 520 mm ML are some 1.8 – 2.0 mm/day (Rosenberg et al., 1981; Lordan et al., 2001). Russian studies in this area demonstrated that squid hatched on the Mid-Atlantic ridge in winter were of 3-10 mm ML at age 20-60 days. In June, when these squids migrate to Hatton – Rockall Basin and Reykianes ridge, their size was already 150-190 mm

(age 160-180 days). In August (Faeroe-Shetland Basin) they grow to 200 – 250 mm (age 190-210 days). In September – October they reach Norway and west Barents Sea at 320-360 mm ML and grow there to 390-420 mm by the end of November – early December (age 290-310 days) before migrating back to the spawning grounds (Sennikov et al., 1986). The mean growth rate between 150 and 420 mm ML in this case might be estimated as 1.8 mm/d, which is very similar to previous results.

Squid growth in Norwegian waters is very intensive – five tagged squid recaptured after 66 days had more than doubled their weight achieving average 1.9 kg BW (Wiborg et al., 1982).

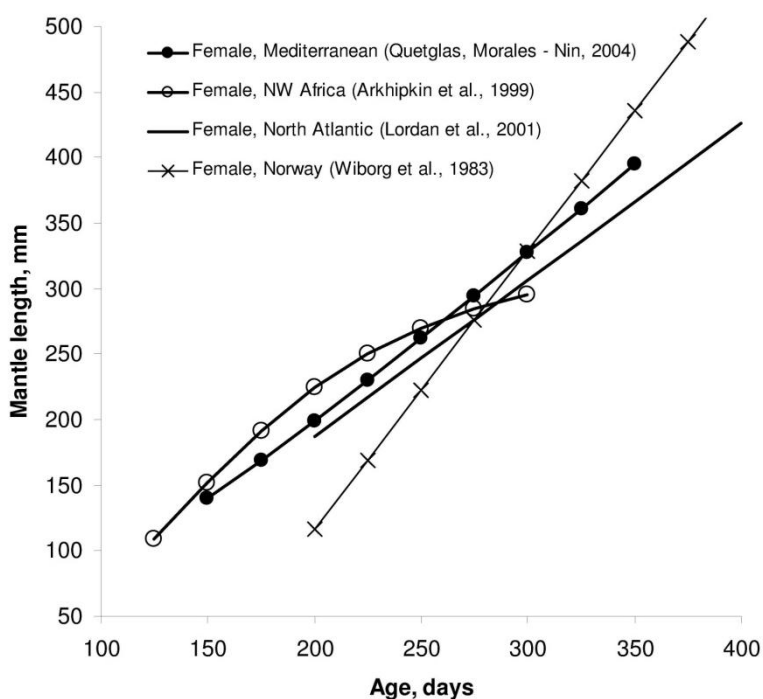


Figure 5. Growth in females of the different populations reconstructed from equations provided by authors.

In the Mediterranean Sea daily growth rates of squids aged 150 - 330 days were ~0.8-1.2 mm/d and 2.5-7.6 g/d in males and 1.1-1.8 mm/d and 2.6-20.5 g/d in females. In the Northwest African population growth rates were 0.5-1.5 mm/d 1.4-3.8 g/d in males and 0.8-1.8 mm/d 3.5-5 g/d in females (Arkhipkin et al., 1999; Quetglas and Morales – Nin, 2004).

Growth rates differ between squid populations and obviously depend on environmental temperatures (Quetglas and Morales – Nin, 2004). Before age of 200 days the fastest growth rates were for African females, and the slowest for squids collected off Norway (Figure 5). Squids from the Mediterranean and around the British Isles occupied intermediate positions. At age 230-250 days African females begin to mature and their growth rates decrease, so they are quickly overtaken in terms of mantle length first by the Mediterranean, and then by the North Atlantic squids. Norwegian squids foraging in the coldest waters are slowest to grow and are the smallest among representatives of all populations at age 200-250 days, but

become the largest at age > 300 days because of delayed maturation. When most Northwest African squids and at least a half of Mediterranean females are already mature (Arkhipkin et al., 1999; Quetglas and Morales-Nin, 2004), almost all squid foraging off Norway are still far off maturity. Surprisingly, at age of ~ 300 days females of all populations are of ~300 mm ML. This might be explained by genetic restrictions on individual growth combined with the annual life cycle in all parts of the species range.

Length – weight relations for squids from the different areas are given in Table 1. There is a noticeable decrease in *b*-coefficient with decreasing latitude (more northern females put more weight on at the same increase in length). This might be explained by greater metabolic energy expenditures with increases in temperature.

Table 1. Relations between length (ML) and weight (W, g) by sex in *Todarodes sagittatus* from different latitudinal parts of the species range (W=a ML^b)
ML measured in centimetres

Region	Sex	a (10 ⁻³)	b	r	Source
Shetland Is.	♂	5.195	3.445	0.987	Joy, 1990
	♀	5.805	3.407	0.990	
Mediterranean Sea	♂	11	3.282	0.987	Quetglas et al., 1998
	♀	9	3.334	0.996	
Northwest Africa	♂	34.3	2.845	0.986	Nigmatullin et al., 2002
	♀	32.6	2.991	0.986	

Table 2. Regional differences in maturation rates of the squid *Todarodes sagittatus*

Region	Min. size (age) of mature squid, mm ML (d)		Size (age) at 50% maturity, mm ML (days)		Source
	Male	Female	Male	Female	
Norway	340	420	>340	>340	Wiborg and Beck, 1983
British Isles	>280	310 ¹	340	~480 ²	Lordan et al., 2001
Mediterranean	196 (222)	318 (257)	232 (245)	337 (300)	Quetglas et al., 1998; Quetglas and Morales – Nin, 2004
NW Africa	200 (184)	250 (208)	(<220)	(230-250)	Arkhipkin et al., 1999; Nigmatullin et al., 1998

¹ some females might remain immature at 500 mm ML (Lordan et al., 2001).

² rough estimation from the graph in the paper by Lordan et al., 2001.

Tropical *T. sagittatus* have a smaller digestive gland – 3-4% BW (Laptikhovsky, unpublished) vs. 3-7% BW in the Mediterranean population (Quetglas and Morales – Nin,

2004) and 4.5-11.9% BW off Faroes and Norway (Wiborg et al., 1982; Wiborg and Beck, 1983).

2.3. Maturation and Fecundity

2.3.1. Regional Differences in Maturation Rates

Rates of maturation and size at maturity also depend on environmental temperatures and vary between populations. Males mature earlier and at smaller sizes than females. Minimum size of mature animals and size at 50% maturity decrease with latitude (Table 2).

2.3.2. Spawning Grounds and Seasonality

Spawning takes place outside of shelf waters. A major spawning centre of the North Atlantic population is situated on the Mid - Atlantic ridge between Azores and 45°N (Sennikov et al., 1986). Another unambiguous spawning site was found in August 1996 on the western side of Porcupine Bank off the west coast of Ireland, at depth of 650 m (Lordan et al., 2001). Portuguese squids probably have a different origin (Borges and Wallace, 1993). Spawning grounds of the North African population are situated at 15- 24°N. Mature females were caught there between 105 and 1,085 m, but mostly at 600-800 m (Nigmatullin et al., 1998). Some reproduction may take place on the slope below 500 m all along subtropical – temperate European and North African shores.

Estimates of the exact timing of spawning peaks differ between areas and authors. The estimations could be biased by sampling time and place, as well as variable between years. Juveniles collected over the mid-Atlantic ridge hatched mostly in December – March, and this was the hatching peak as well of squids collected in Norwegian and Barents Sea by Russian scientists (Shimko, 1984; Sennikov et al., 1986). Squid sampled in July – September in north Norwegian waters hatched between October and February with December peak. Squid from southern Norway collected during the same period had the hatching peak in January. Squid sampled in the region of Hebrides – Rockall – Porcupine bank in March – April had a hatching peak in June (Wiborg and Beck, 1983). Scarce data on statolith reading by Rosenberg et al (1981) hint at two hatching peaks – in May and October.

Two hatching peaks, May – July and December – February, were found in waters around the British Isles, where mature females occurred in catches from March to November (Lordan et al., 2001). Hatching occurred throughout the year in the Mediterranean Sea, but mostly in August - December with November peak. This also corresponds to the peak of maturity in September - December (Quetglas et al., 1998; Quetglas and Morales – Nin, 2004).

Around the Canary Islands and off Northwest Africa mature mated and spent females were found between November and February (Piatkowski et al., 1998; Nigmatullin et al., 1998; 2002). Squid captured during the period of mass abundance in summer were hatched between December to August with February – March peak (Arkhipkin et al., 1999).

It is possible to conclude that the species is characterised by year-round spawning with a strong winter peak. The winter-spawning cohort represents the only squids that penetrate far north into Norwegian and Barents Seas to forage. A cohort reproducing in late spring – early summer is important only in the North Atlantic population.

2.3.3. Male Reproductive System

The male reproductive system has a typical morphology of an ommastrephid squid (Nigmatullin et al., 2003). Relative spermatophore size likely varies between populations – it was found to be about 9-10% of ML (20-29 mm) in Northwest African squids of 245 and 248 mm ML (Sabirov, 1995) and ~ 20% (48-54 mm) in Mediterranean squid of 260 mm ML (Mangold – Wirz, 1963). It is 38 – 44 mm in the North Atlantic squids (Roper et al., 2010). Spermatophore morphology is typical for that of *Todarodinae* with a seminal reservoir consisting of two parts (Sabirov, 1995). In two Northwest African squids with 33 and 145 spermatophores respectively the seminal reservoir was about 1/3 of spermatophore length and mean 4.1% ML. Spermatophore weight varies between 10 and 17 mg (Sabirov, 1995). Spermatozoa head length is 7.5-8 µm, tail length is 100-120 µm (Laptikhovsky, 1990).

2.3.4. Female Reproductive System and Fecundity

Potential fecundity of this species is some 200,000 – 900,000 eggs in the Northwest Africa population, and attains at least 2,370,000 in the Mediterranean Sea (Laptikhovsky and Nigmatullin, 1999). Numbers of yolky eggs (protoplasmic oocytes ignored) in North Atlantic animals varied from 205,000 to 532,000 (Lordan et al., 2001). Females have 16-33 (mean 28) seminal receptacles on the buccal membrane to store sperm for fertilisation (Nigmatullin et al., 1998). Ovary maturation is asynchronous providing a possibility of intermittent spawning. Oviducts' capacity is several times smaller than the potential fecundity. Mature females from Northwest Africa (ML 253-341 mm) had 14,000 – 76,000 ripe eggs in oviducts, animals caught in Irish, Scottish and Norwegian waters (ML=415-520 mm) had 77,500 - 130,300 eggs (Wiborg and Gjørøster, 1981; Laptikhovsky and Nigmatullin, 1999; Lordan et al., 2001). It indicates that each female might have several (perhaps up to ten) spawning events in its lifetime separated by short periods of accumulation of new eggs in the oviduct.

The mean largest diameter of ripe eggs was 1.1 mm in smaller animals caught off Northwest Africa (Laptikhovsky and Nigmatullin, 1999), 0.9-1.4 mm (mean 1.2 mm) in larger squids sampled in the Irish and Scottish waters (Lordan et al., 2001), and 1.1 mm in a very large Mediterranean female (Cuccu et al., 2005), so it seems to be equal across the species range. Much larger values however were indicated for Norwegian waters - 1.5 – 1.7 mm (Wiborg and Gjørøster, 1981; Shimko, 1984) and for waters of the Shetland Islands – 1.7-2.6 (mean 2.0) mm (Joy, 1990). The discrepancy probably happened because in the latter cases authors worked with frozen rather than preserved materials (Lordan et al., 2001). Reported egg sizes of 1.9-2.4 mm in animals from the Mediterranean Sea (Mangold – Wirz, 1963) contradict recent findings (Cuccu et al., 2005) and also might represent measurements of frozen samples, but this cannot be ascertained. Egg weight in West African squids is 0.37-0.42 mg (Nigmatullin and Laptikhovsky, 1999).

3. Ecology

3.1. Distribution and Abundance

It is a nerito-oceanic North-East Atlantic species that occurs from the southern edges of the Arctic Ocean (Barents and Kara Sea, Iceland) southward to Guinea (10°45' N) including

the North Sea and the Mediterranean Sea. In the North Atlantic its range extends westward to the mid-Atlantic Ridge, and eastward through the entire Mediterranean Sea into the Marmara Sea (Katagan et al., 1993; Nigmatullin et al., 1998; Roper et al., 2010). A range of international bottom trawl surveys in Guinea Gulf failed to find the species, though two other shelf ommastrephids – *I.coindeti* and *T.eblanae* were present in the area (Ch.M.Nigmatullin and M.Vecchione, pers.comm). It occurs from surface to the bottom down to >1000 m and in surface waters it can forage above depths > 4,000 m (Roper et al., 2010).

Reports on its occurrence in the southern hemisphere down to Angola (Roper et al., 2010; WoRMS, 2011) and even Southwest Indian Ocean (EOL, 2011) are probably based on confusion with *T. angolensis* and *T. filippovae*, particularly because in some biodiversity databases the former is still considered to be a subspecies, *T. sagittatus angolensis* (WoRMS, 2011).

Abundance of the species is highly variable both seasonally and throughout the species range. In the North Atlantic (south of Iceland, the Faroe Islands, Norway, and in some years, Scotland) large schools appear in early summer and remain there until the beginning of winter. (Roper et al., 2010). In the Mediterranean Sea *T. sagittatus* is distributed more or less evenly, and areas of large aggregations or abundance explosions are not known. Off Northwest Africa the zone of maximum abundance is situated on the continental slope off the Cap Blanc upwelling area (19-23°30' N) where sometimes the species occurs in large numbers (Nigmatullin et al., 1998). Between 24°N and the Gibraltar Strait species abundance is very low, indicating a gap in distribution.

3.2. Migration/Horizontal Movements

The North Atlantic population of *Todarodes sagittatus* is migratory and undergoes important spatial seasonal migrations between spawning grounds and foraging areas. Squids born in winter on the mid-Atlantic ridge and on the western continental slope of Europe are dispersed into northern waters, usually appearing in Icelandic and Faroese waters in the summer and then, later on – around the Shetland Islands and in Norwegian waters, which they enter from the north at age ~ 10 months. After a period of foraging they descend back to the spawning grounds (Wiborg and Beck, 1983; Sennikov et al., 1986; Joy, 1990). Males being of smaller size and having lower speed than females can not migrate as far away from spawning areas, and because of this the sex ratio is biased towards females all over the foraging area (Zuev et al., 1976; Borges, Wallace, 1993). Males possibly remain on the spawning grounds without taking part in the feeding migrations (Roper et al., 2010).

Mediterranean and Northwest African populations probably are rather stationary, at least there are no evidence of distant migrations across the area but ontogenetic descend to bigger depth with maturation (Nigmatullin et al., 1998).

3.3. Vertical Migrations

T. sagittatus is known to carry out two types of vertical migrations: 1) diel vertical migrations between the surface and near-surface waters at night and in proximity to bottom

waters during the day and 2) ontogenetic migration down to the slope, which also represents a horizontal movement.

From manned submersibles “Sever-2” this species was observed on the North Atlantic Ridge (49-55°N) between 530 and 1,947 m some 2-10 m above the bottom in the daytime, and near the surface at night. Squid size was 100-500 mm, mostly 150-350 mm ML (Moiseev, 1991) so presumably most if not all were immature and maturing. Similar occurrence was found in the Northwest African population in which juveniles and immature squids of 60-250 mm ML (mostly 140-180 mm ML) were found in numbers in surface waters at night, but were completely absent there during day although caught at the bottom. These vertical migrations cease with squid maturation as adult squids switch to a demersal life style (Nigmatullin et al., 1998).

Ontogenetic vertical migration has been observed at least for Northwest African and Mediterranean populations. Paralarvae and early juveniles of this species < 80 mm ML are distributed in surface waters above the continental slope (Nigmatullin et al., 1998). Upon growing they swap this habitat for waters of the shelf edge. This occurs at squid size of about 100-200 mm ML. During further growth and maturation animals gradually move deeper, so mean size increases with depth, and mature animals are generally caught deeper than 500 m (Nigmatullin et al., 1998; Quetglas et al., 1998). It is not the obvious case for the North Atlantic population, of which early juveniles were captured above the mid-Atlantic ridge in the open ocean (Sennikov et al., 1986) and large immature squid forage so close to shore that they are often stranded in great numbers at low tide (Sennikov et al., 1986; Roper et al., 2010).

3.4. Feeding Ecology and Behaviour

Feeding spectra of *T. sagittatus* vary between different parts of the species range and are well studied throughout it. In Icelandic waters *T. sagittatus* preys mostly on pelagic fish like blue whiting *Micromesistius potassou*, red fish *Sebastes* sp, and *Chauliodus sloanei* (Jonsson, 1998). In the north of Norway (66-70°N) and in the Barents Sea this species consumes in numbers a variety of different pelagic fishes including schooling species: herring *Clupea harengus*, capelin *Mallotus villosus*, blue whiting, and sand eel *Ammodytes tobianus*, as well as redfish and small cod, *Gadus morhua*. Other pelagic prey are polychaetes (mostly *Nereis pelagica*), crustaceans (mostly euphausiid *Meganyctiphanes norvegica* and shrimp *Pasiphaea* sp) as well as copepods. Squids smaller than 33 cm ML mostly fed on crustaceans, whereas animals >33-50 cm ML mostly fed on fish and its importance in the diet increased with predator size. Cannibalism is also common (Wiborg, 1972; Wiborg and Gjørsater, 1981; Wiborg and Beck, 1983; Sennikov et al., 1986).

In southern Norway (60-66°N) squid consume mostly fish, namely *Maurolicus muelleri* and redfish. Blue whiting, saithe *Pollachius virens*, Norway pout *Trisopterus esmarkii*, and silver smelt *Argentina silus* are of lesser importance. Amphipod *Parathemisto* sp are also preyed upon (Wiborg, 1972; 1978; Wiborg and Beck, 1983).

In Faroese waters sand eel and blue whiting are the most common fish prey, though herring and redfish are also consumed. Unidentified jellyfish was found in >50% of stomachs; shrimps, chaetognaths and pteropods *Clio* sp. were scarce (Wiborg and Beck, 1983).

Pelagic fish (mostly *Maurolicus muelleri*, blue whiting and silver smelt, *Argentina* sp) predominated in squid diet around the British Isles. Prawns and pteropod *Limacina retroversa* were only important among invertebrates (Wiborg, 1972; Lordan et al., 2001). In the Shetland Islands area the most important fish prey were Norway pout and whiting *Merlangius merlangus* (Joy, 1990) as well as demersal haddock, *Melanogrammus aeglefinus* was identified in squid stomach contents from the Scottish waters (Pierce et al., 1994).

Pelagic fish was also the most common prey in the Mediterranean Sea. Those were myctophids (dominated by *Ceratoscopelus maderensis*), *Notolepis rissoi* and *Lepidopus caudatus*. The second important group was crustaceans, particularly red shrimp, *Aristeus antennarius*. Cephalopods constituted the third important group, including cannibalism. Because larger squid generally occur in deeper waters, with increasing animal size shelf fish decrease in importance in the diet whereas mesopelagic fish and shrimps increase (Quetglas et al., 1999).

In the southern areas (Canary Islands, Morocco, and Mauritania) fish remain the most important prey and are represented mostly by myctophids. This is followed by shrimps (*Plesionika* spp, Sergestidae, Palaemonidae and Pandalidae) and other crustaceans like euphausiids, amphipods, Galatheididae, and copepods. Oegopsid squid are consumed in small numbers (Hernandez – Garcia, 1992; Piatkowski et al., 1998; Nigmatullin et al., 2008).

Comparison between these diet spectra show that in the Northeast Atlantic squids forage mostly in shelf waters, whereas in the Mediterranean Sea and off Northwest Africa they forage mostly over the continental slope.

Cannibalism is very common with larger squid consuming considerably smaller conspecifics. In Senja fjord in North Norway the frequency of squid in stomachs increased strongly from October to November, while that of fish decreased. It is supposed that when the squid enter fjords, the available fish are eaten first and then, when food gets scarce, squid switch to cannibalism (Wiborg, 1972). However, it could sometimes be a consequence of aggressive behaviour when squids are aggregated in the light field of a jigger or inside a trawl net (Wiborg and Beck, 1983; Quetglas et al., 1999; Lordan et al., 2001).

Among other cephalopods consumed by *T. sagittatus* are Sepiidae, Sepiolidae, *Gonatus* spp, *Illex coindetii*, *Thysanoteuthis rhombus*, *Todaropsis eblanae*, *Brachioteuthis* sp. and Cranchiidae (Joy, 1990; Piatkowski et al., 1993; Quetglas et al., 1999; Lordan et al., 2001). Generally cephalopods are of a small importance in the squid diet, but are sometimes locally important (Wiborg, 1972).

It is evident that *Todarodes sagittatus* is an omnivorous predator that will feed on any kind of live prey it can cope with, including smaller conspecifics. Its feeding spectra mirror the micro- and mesonekton composition, diversity, and abundance in pelagic waters. Generally the squid feeds on fishes, crustaceans and cephalopods in decreasing order of importance. Benthic prey appears in stomach of larger squids when they switch to demersal life after maturation.

Prey size increases with squid ML and larger individuals also consume wider ranges of prey sizes (Wiborg and Beck, 1983; Breiby and Jobling, 1985; Quetglas et al., 1999). The most intensive feeding takes place during the day. In night most stomachs are empty or contain little food (Wiborg and Beck, 1983).

3.5. Predators

The most specialised fish predator of *T. sagittatus* in the Northeast Atlantic is swordfish. The squid is also consumed by sharks and rays, tunas, hake, coalfish, large cod, seabasses, Greenland halibut, and lancetfish (Forster, 1967; Zuev and Nesis, 1971; Stevens, 1973; Guerra et al., 1993; Hernandez – Garcia, 1995; Hovde et al., 2002; Maia et al., 2006; Logan et al., 2011). It has also been recorded in harp seal diets (Bjørge et al., 1981) and in stomachs of Cuvier's beaked whales, sperm whales, pygmy sperm whales, and different dolphins, among which Risso's dolphins and long-finned pilot whales are specialised squid-eaters (Clarke and Pascoe, 1985; Gonzales et al., 1994; Santos, 1998; Abollo et al., 1998; Arronte et al., 2009; Spitz et al., 2011). In years of high squid abundance, pilot whales have migrated through the Iceland–Faroe region and approached the Faroes from the north apparently following this prey (Sundet, 1985; Bloch et al., 2003; Hátún et al., 2009). Juvenile squids foraging in surface waters are also important food of some seabirds, like Manx shearwaters and Cory's shearwaters (Croxall and Prince, 1996).

In the Mediterranean Sea and subtropical East Atlantic *T. sagittatus* is the most important cephalopod prey in the diet of swordfish, which feed on juvenile and sub-adults of 63-336 mm ML, mostly 170 -270 mm. It is also preyed upon by other billfishes, tuna, sharks and rays (Bello, 1991; Hernandez – Garcia, 1995; Salman, 2004; Peristeraki et al., 2005; Romeo et al., 2011; Valls et al., 2011). Squids of size similar to that in the swordfish diet represent the bulk of cephalopod prey of the dolphin fish, *Coryphaena hippurus* (Massuti et al., 1998), whereas Albacore tuna and chub mackerel feed mostly on early juveniles (Bello, 1998; Castro, 2001). In this area the squid is also one of the most important cephalopod preys of pilot whales and different dolphins (Hernandez – Garcia and Martin, 1994; Blanco et al., 2001; Bearzi et al., 2011).

In deep seas *T. sagittatus* occasionally has been found in the diet of grenadiers, sharks and rays. However, at least in some cases this could be the result of scavenging (Gushchin and Podrazhanskaya, 1985; Carassón et al., 1992; Martin and Christiansen, 1997).

3.6. Parasites

T. sagittatus is an important paratenic host for anisakid nematods – parasites dangerous for human health if not killed by freezing or cooking. Because their final hosts are marine mammals, these nematodes do not develop in the human body, but can survive and even one larva is sufficient to provoke strong symptoms of a disease – anisakidosis (Gaevskaya, 2005). Prevalence of the genus *Anisakis* generally varies between 20 and 70% in commercial size squid, but is very low in small sized animals sampled in African waters (Table 3). A sharp increase of parasite prevalence in squids > 200 - 300 mm ML is particular for ommastrephids and is caused by ontogenetic changes in the diet. Anisakid numbers and occurrence in squid also depend on the abundance of marine mammals (Nigmatullin and Shukhgalter, 2006). Pilot whales – likely the most abundant specialised squid eaters among cetaceans of the Northeast Atlantic - prey on relatively large *T. sagittatus* of mean size 255±78 mm ML (Spitz et al., 2011).

Table 3. Infestation of *T. sagittatus* by *Anisakis* spp in different parts of the species range

Area	Squid size (ML mm)	Prevalence (%)	Intensity	Source
NE Atlantic Scotland	170-420	62	3.8	Smith, 1984
NE Atlantic, Spain	255-400 (334)	34.3 and 33.8	7.6 and 0.39	Abollo et al. 1998; 2001
Mediterranean Sea, Sardinia		20	1	Angelucci et al., 2011
Mediterranean Sea, Tunisia		76.5		Farjallah et al., 2008
NE Atlantic, Morocco and Mauritania	115-320 (mostly < 200)	0.3	1	Nigmatullin and Shukhgalt, 2006

Among other parasites of the Northeast Atlantic and Mediterranean populations are the anisakid nematodes *Hysterothylacium* spp, cestodes *Phyllobothrium loliginis*, *P.dolhri*, *Nybelinia lingualis*, and *Amphistoma loliginis*, infusoria *Chromidina*, coccidian parasites *Aggregata sagittata*, digenetic trematodes Didymozoidae, as well as gill-infesting copepods *Pennella* and probably dicyemids (Zuev and Nesis, 1971; Overstreet and Hochberg, 1975; Gestal et al., 2000; Pascual et al., 2005).

Detailed study of the helminth fauna off Northwest Africa revealed several parasite species: Trematoda: Didymozoidae (prevalence 40.9%, intensity 1–10), *Hirudinella ventricosa* (0.5%, 1); Cestoda: *Scolex pleuronectis unilocularis* (22.3%, 1–2), *S. pleuronectis bilocularis* (3.2%, 1), *Phyllobothrium* sp. (1.1%, 1); Nematoda: *Porrocaecum* sp. (0.5%, 1), and *Spinitectus* sp. (4.2%, 1–2). All helminths found were at the larval stage. Because arrow squid play an important role in pelagic and demersal ecosystems as II–IV order consumers, they are important transient hosts for helminth transfer from invertebrates (primary hosts) to small teleosts (intermediate hosts) and to sharks, large teleosts, and mammals (definitive hosts) (Nigmatullin et al., 2008).

4. Fisheries

4.1. Stock Definition and Fishing Areas

Because of differences in squid ecology in the different parts of the species range and isolation between them, it is estimated that there are at least three populations: 1) Northeast Atlantic population 2) Mediterranean population, and 3) Northwest African population (Nigmatullin et al., 1998; Roper et al., 2010). Wiborg and Beck (1983) inferred also that within the Northeast Atlantic population there are two stocks migrating to forage in Norwegian waters: one hatching during winter, and the other in early summer. This is in agreement with data from the Northeast Atlantic (Scotland – Ireland area), where one cohort was present in the early months of the year, and the second cohort appeared in summer and persisted until December (Lordan et al., 2001).

Status of these populations and stocks is unclear because genetic comparisons between them have not been researched.

T. sagittatus is currently taken as bycatch throughout the species range with no major fishing areas existing nowadays, but it has periodically occurred in Norway in sufficiently large numbers to support a moderate target fishery (Pierce et al., 2010). A specialised trawl fishery also took place in waters off South Morocco and Mauritania, but this happened just once – in the summer of 1974 (Nigmatullin et al., 1998).

This squid is consumed fresh or boiled, marketed frozen, salted or dried, and is used as bait in the cod and halibut fisheries (Roper et al., 2010).

4.2. Fishing Methods and CPUE

Fishing methods that catch *T. sagittatus* depend on the area, but were invariably designed to catch something else. The most important is bottom trawling, in which this species is taken as a small bycatch around Europe from Greece to Scotland and Norway (Roper et al., 2010). The squid is also taken by gillnets off France and north Spain, purse-seines and Scottish fly-seines off the United Kingdom, gill-nets and trammel nets off Portugal, hand-jigs around Italy, and hand-jigs, purse-seines and trammel net in Greece (Pierce et al., 2010).

In the 1980s *T. sagittatus* was caught as bycatch during the commercial purse seine fishery for pollock, mackerel and herring off Norway and in the northern North Sea. Amounts varied from several kilograms to 50 tons per day. However, an experimental target fishery in Norway in October – November 1981 was a failure. Squids were located by echo – sounder and concentrated with lights mounted on a small anchored skiff. Unfortunately, they were attracted in low numbers, and the maximum catch was ~ 200 kg (Wiborg et al., 1982).

Jigging turned out to be more successful. During the same period a prawn trawler was equipped with 5 jigging machines with double line drums. During 6 weeks of fishery the maximum daily catch was 3.3 tonnes, whereas another trawler equipped with 8 single-line drum jigging machines caught 100 tonnes of squid during the month with maximum catches of 10-12 t per day. Attempts to use Japanese drift nets for this squid fishery in Norway were not successful (Wiborg et al., 1982; Wiborg, 1983).

An experimental jigger fishery in Soviet waters of the Barents Sea in autumn 1981 resulted in 1 - 10 t of squid per night. In April – May 1982 trawlers fishing for blue whiting took up to 4 t of squid per week as bycatch, but generally an attempt to launch a specialised trawl fishery there in 1980s failed because of low catches (Wiborg, 1983, PINRO, 2011).

Pelagic nets for some reason do not concentrate the squid into the trawl path as they do with *Illex* and *Loligo* (PINRO, 2011). Most of the squid (210-470 mm ML) in catches of research hauls by a semi-pelagic commercial blue whiting trawl were found in meshes of the wings of trawl, and very few in the codend (Wiborg and Beck, 1983). The same situation occurred during Russian research surveys off Northwest Africa when a semi-pelagic net (vertical opening ~30 m, horizontal opening 40-50 m, mesh size 10-34 mm) was used. Squid size in catches was mostly 120-240 mm ML, and most of the catch was stuck in the wings.

All over the Mediterranean Sea (mostly around Italy) the squid is taken as a minor bycatch by trawlers working on the continental slope, usually between 200 to 800 m. In the Balearic Sea this species is mainly fished by trawlers targeting red shrimp (*Aristeus antennatus*) and Norway lobster (*Nephrops norvegicus*).

Catches of *T. sagittatus* by commercial trawlers both in east and west Mediterranean generally are <1 kg/hr all year round. (Sundet, 1985; Ragonese and Bianchini, 1990; Quetglas et al., 1998, 2000; Politou et al., 2003 ; Lefkaditou et al., 2003).

Off Northwest Africa the squid was fished as an important bycatch of Russian trawl fisheries for pelagic and demersal fish (chub mackerel, horse mackerel, hake and others) from Cap Blanc to 23°N – 23°30' N. Normally catches peaked at 300-500 kg/day in June – July, though in years of high abundance some vessels could achieve 2-6 t/day and even 10-15 t/d. The best catches were obtained on the bottom between 10 a.m. and 5 p.m. Because fish predominated in catches, particularly horse mackerel, commercial freezing of whole squid was often hampered by intensive skin damage.

Production of canned pieces of mantle and arms turned out to be an optimum solution to the problem. In 1992 Russia recognised Moroccan jurisdiction of these waters, and a sporadic squid fishery was stopped (Nigmatullin et al., 1998). The species was also taken occasionally by the Russian fleet in Mauritania before 1983, when the country introduced a prohibition on cephalopod bycatch.

4.3. Landings

Landings of the squid are very variable throughout the species range and peaks of catches generally lasted just a few years followed by long period of low squid abundance.

During the last 60 years reported squid catches varied from nil to ~20,000 t (Figure 6), mean 2,934 t for a period 1950-2009. Among those a mean annual 1,904 t were taken in Norway.

The maximum reported catch in Norwegian waters was ~ 18,000 t in 1982 – 1983, and after 1988 commercial aggregations disappeared from the area (FIGIS, 2011)

In the Northeast Atlantic and in the Mediterranean Sea the species is taken as bycatch together with other ommastrephid squids, *Illex coindetii* and *Todaropsis eblanae* and sometimes *Ommastrephes bartrami*.

All of them are often reported together as unidentified squids. Since 1980 the catch of these three species combined varied in the NE Atlantic from 4,018 to 13,440 t (mean 8,119 t) and in the Mediterranean – from 3,000 to 8,856 t, mean 5,742 t (FIGIS, 2011). Annual mean by catch by Italian bottom trawlers – the most important fishery for the species in the area - was estimated as ~3,000 t (Pierce et al., 2010).

In Mauritanian waters, a total of 18,000 t was taken by Russian trawlers during the explosion of abundance in the summer of 1974. In 1975 Mauritania introduced the exclusive economic zone and annual catches fell to 500-3,000 t between 1976 and 1982. In waters of the former West Sahara 17 – 3,725 t per annum were taken by Soviet trawlers in 1980-1991; mostly in July and August (Nigmatullin et al., 1998). Nowadays neither Mauritania nor Morocco reports separate statistics for this species.

Total annual catch of all squids combined (mostly *Loligo vulgaris*, but also ommastrephids including *T. sagittatus*) ranged between 2,114 – 8,456 t in 2005-2009 (FIGIS, 2011).

Generally, mean recent annual catches of the species over the entire range from Mauritania to Norway may be estimated as 10,000 – 15,000 t (about 1% of the biomass

consumed by pilot whales – see below). However, during sudden explosions in abundance the total catch may achieve 15,000 – 20,000 in relatively restricted areas.

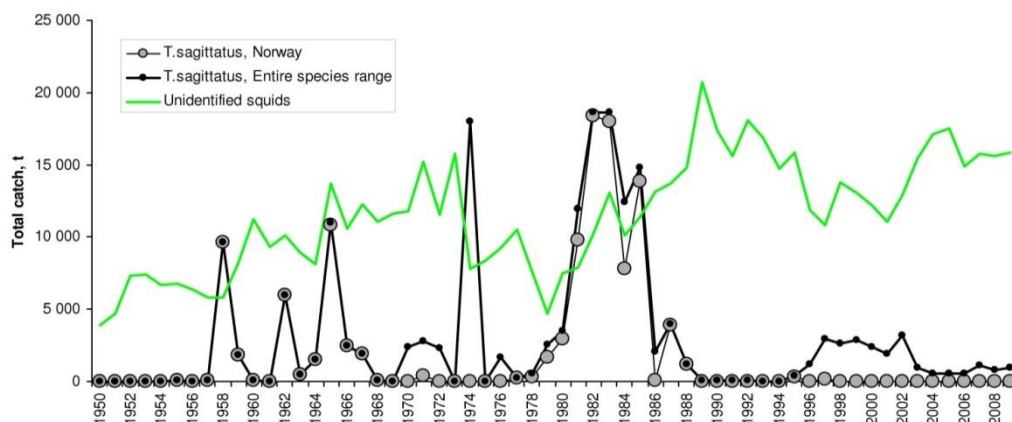


Figure 6. Landings of *T.sagittatus* and unidentified squids in the area of the species regular distribution (FIGIS, 2011).

4.4. Recruitment and Environmental Variability

Recruitment of the squid and its abundance are highly variable and presumably depend on a range of oceanographic factors. Explosions of abundance in the North Atlantic when the species invaded Norwegian and Barents Seas – the world’s largest fishery grounds for this species - occurred in 1885, 1891, 1930- 1931, 1937-1938, 1949, 1958, 1962 and 1965 (Zuev, Nesis, 1971). The next period of very high squid abundance occurred in 1981-1985 and since then squid abundance in northern waters became low.

It was found that the reported catches in Norwegian and Barents Sea were not correlated with the abundance of *Salpa fusiformis* (an indicator of the strength of North Atlantic Current, NAC). A negative correlation was found between *T. sagittatus* abundance and mean temperature in the upper 200-m layer on the transect North Cape - Bear Island (Nordkapp - Bjørnøya) in September. Catches were higher when the surface water temperature anomaly in January-March and the index of meridional atmospheric circulation in February-April were both positive, and these could be used for fishery forecast in northernmost waters with four month advance (Berenboim et al., 1992). However, these data show an impact of environmental variability on stock distribution rather than on its size.

4.5. Management and Stock Assessment

No specific management measures are presently applied to the species (for a review of actual cephalopod fisheries management practice in Europe, see Pierce et al., 2010).

Total standing biomass of *T. sagittatus* over the entire range was estimated at ca. 1-2 mln t following some analytical consideration of data on species landings and CPUEs (Nigmatullin, 2004). Unpublished survey data from R.V. “AtlantNIRO” (Sidi and Guénette,

2004) provided assessment of the biomass of this species in Northwest African waters as 30,000 t. Abundance of the species in the Mediterranean Sea is generally low. Densities of the squid in waters around Sardinia (Mediterranean Sea) in a narrow band between 400 and 800 m were estimated in 1994-2003 as 1-6 kg/km² without an obvious trend, although small numbers of the species were also distributed shallower and deeper (Cuccu et al., 2005).

Total production of the species is much higher than standing biomass because P/B coefficient values in inshore squids are about five (Nesis, 1985), and could be estimated from the species consumption by predators, in particular pilot whales and sperm whales.

The bulk of food (~80%) consumed by long-finned pilot whales in the Northeast Atlantic is cephalopods, and mean weight of these cetaceans is 789 kg (Clarke, 1996; Sigurjónsson and Víkingsson, 1997). *T. sagittatus* accounts for 17.2% by weight of squids and octopods consumed by this species (Spitz et al., 2011). Total number of whales in waters east of Greenland (i.e. Northeast Atlantic) was estimated as 778,000 (Buckland et al., 1993). Several empirical models (review – Barlow et al., 2008) predict that pilot whales' daily food consumption should be ca. 5% BW. All these numbers together provide an estimation of annual food consumptions of commercial-sized *T. sagittatus* as 1.5 million t by pilot whales only. Sperm whales consume some 540-2,400 thousand tons of cephalopods in North Atlantic plus 67-437 thousand tons around the Azores, but most of them belong to family Gonatidae (Clarke, 1996; Santos et al., 2001), and *T. sagittatus* represents ca. 0.4% of cephalopod prey by weight (Spitz et al., 2011). Resulting annual consumption of the European flying squid is 2,500 – 11,500 t only. Other cetaceans are even less important as consumers of this species. Because there are no abundant fish predators specialised on *T. sagittatus* other than swordfish, and this species only represents a minor part of other fish diets, the annual consumption of this squid over the entire range could be roughly estimated as 2-3 millions t.

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***Todarodes pacificus*, Japanese Common Squid**

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Abstract

The Japanese common squid, *Todarodes pacificus* (Cephalopoda; Ommastrephidae) is a commercially important squid in Japan and Korea. *T. pacificus* is found to the west of Japan in the Sea of Japan and the East China Sea as well as in the Oyashio and Kuroshio Current Systems off eastern Japan.

There are 3 subpopulations with different peak spawning seasons; summer, autumn and winter, with the later two the largest and most important. The autumn spawning occurs mainly in the southern Sea of Japan, including Tsushima Strait between Japan and South Korea, while winter spawning is in the East China Sea off Kyushu Island south of Japan.

Annual catches have fluctuated widely since the 1990s, with a marked increase occurring after the late 1980s; this increase appears to have been related to a climatic

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regime shift from a cool to a warm regime that occurred in 1988/89. We review *T. pacificus* life history biology, ecology and fisheries.

1. Introduction

The Japanese common squid, *Todarodes pacificus* (Cephalopoda; Ommastrephidae) is a commercially important squid in Japan and Korea. Its Japanese and Korean name is “surume-ika” and “ojingo”, respectively; other local name in Japan includes “ma-ika”. *T. pacificus* is a nerito-oceanic squid, which is found to the west of Japan in the Sea of Japan and the East China Sea as well as in the Oyashio and Kuroshio current systems off eastern Japan.

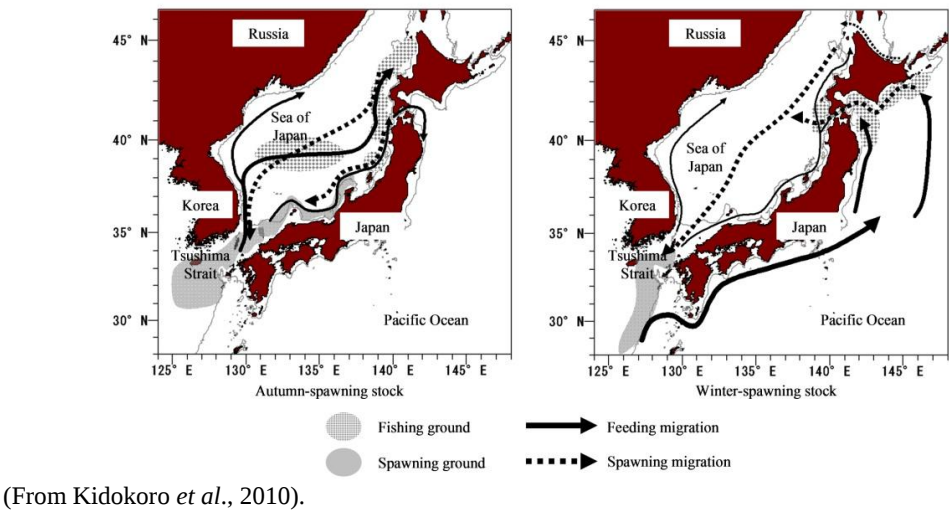


Figure 1. The distribution range and migration pattern of *Todarodes pacificus*.

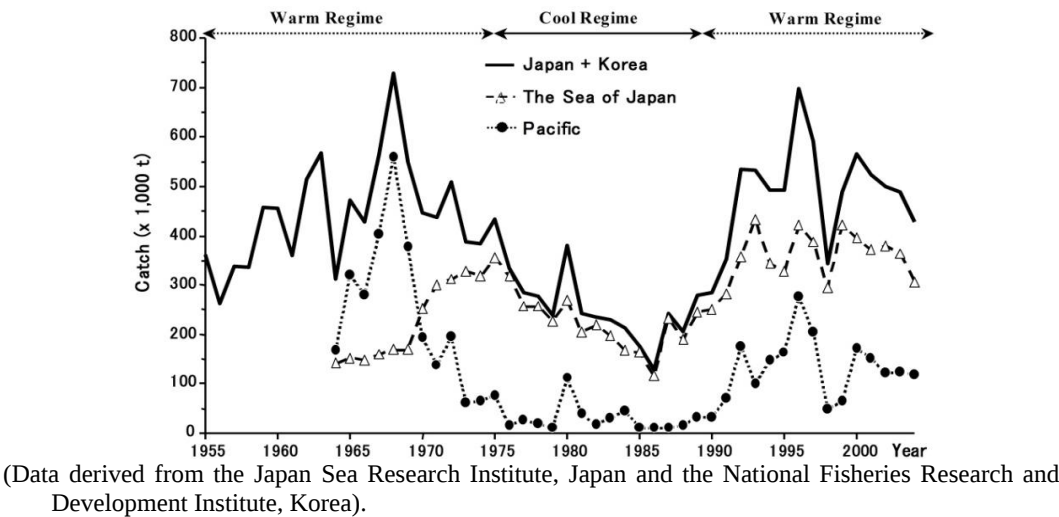


Figure 2. Annual fluctuation in Japanese common squid, *T. pacificus* catches of Korea and Japan during 1955 - 2004.

There are 3 subpopulations with different peak spawning seasons; summer, autumn and winter, with the later two the largest and most important (Figure 1, Murata, 1990; Sakurai *et al.*, 2000). The autumn spawning occurs mainly in the southern Sea of Japan, including Tsushima Strait between Japan and South Korea, while winter spawning is in the East China Sea off Kyushu Island south of Japan. This species has a 1 year life cycle with the autumn spawned squid migrating to the northern Sea of Japan and then back again to spawn before dying. Some of the winter spawned squid migrate to feed in the northern Sea of Japan while others migrate in the waters off eastern Japan to the Oyashio region where they feed during the summer and autumn. Annual catches have fluctuated widely since the 1990s, with a marked increase occurring after the late 1980s; this increase appears to have been related to a climatic regime shift from a cool to a warm regime that occurred in 1988/89 (Figure 2, Sakurai *et al.*, 2000, 2002).

2. Life History Biology

2.1. Early Stages

T. pacificus paralarvae occurred widely in the southwest Sea of Japan, the East China Sea and pacific coast of Japan (Shojima 1972, Okutani and Watanabe 1983, Goto 2002, Goto *et al.*, 2002). The distributions of the paralarvae are associated with the Tsushima Warm Current in the Sea of Japan and the Kuroshio along the Pacific coast of Japan (Okutani and Watanabe 1983, Hatanaka *et al.*, 1985, Bower *et al.*, 1999). Paralarvae shows no large diel vertical migration, and hatching sized paralarvae occurred near surface and as size increases, paralarvae gradually descend in the water column and the variability in depth increases with ontogeny (Yamamoto *et al.*, 2002, 2007).

The development of a technique of artificial fertilization for ommastrephid squids (Sakurai *et al.*, 1995) has made it possible to examine the development and early life stages of *T. pacificus* (Figure 3, Watanabe *et al.*, 1996, Sakurai *et al.*, 1996). After hatching, paralarvae were maintained for up to seven days without being fed while the internal yolk was completely absorbed (Watanabe *et al.*, 1996). Paralarval mantle lengths measured 0.95 mm at hatching and 1.25 mm after seven days. To date, there have been no successful long-term rearing experiments, as all attempts to feed the hatchling paralarvae have failed. Normal embryonic development occurs at temperatures between 14.0 and 26.0°C with highest survival rates occurring between 14.7-22.2°C (Sakurai *et al.*, 1996).

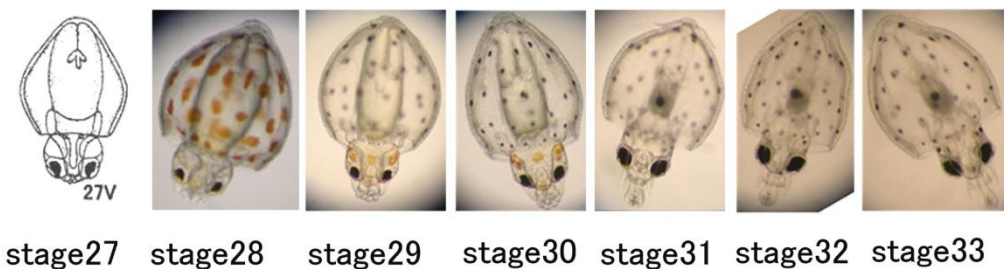


Figure 3. Development stage of hatchling (Watanabe *et al.*, 1996).

While the swimming ability of hatchling increased between 18 and 24°C, especially in 19.5-23°C (Yamamoto *et al.*, 2012) at development Stage 31-32, which was classified by Watanabe *et al.* (1996).

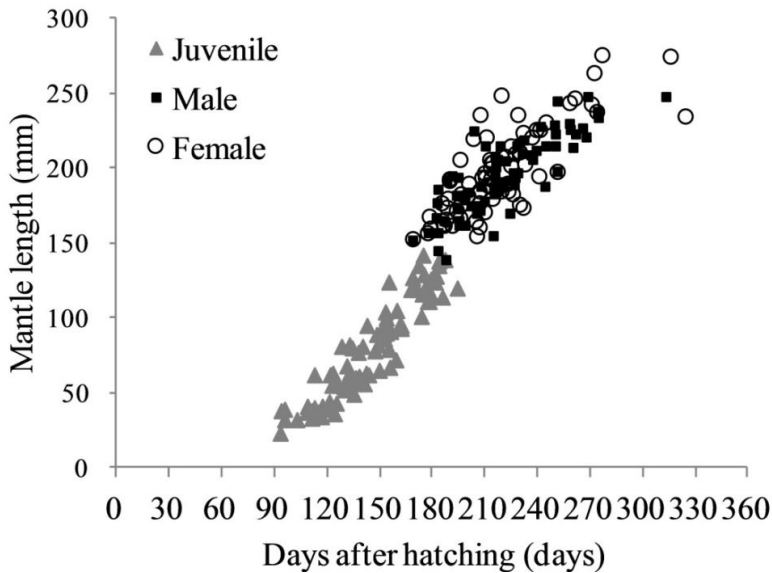
2.2. Age and Growth

The growth of *T. pacificus* had been examined based on the monthly shifts in the mantle length composition of the commercial catches until 1980s (Araya, 1967), and on the growth increments in a statolith microstructure since 1990s (Nakamura and Sakurai, 1993). The growth in the juvenile stage take 4 months to reach 5cm mantle length size after hatching (Figure 4). Then, the growth rate began to increase rapidly after 4 month age, and it is estimated that the age at 20cm mantle length (ML) is about 7 month. There is a difference by sex in the growth rate of individuals of ML above 20cm in which gonads begin to grow in males. Basically, females grow about 1 - 2cm larger than males in the end of their life (Araya, 1967; Kidokoro *et al.*, 1999). The growth pattern of *T. pacificus* was reported to be different in hatching season (Araya, 1967; Okutani, 1983). The ML of the cohort hatched during spring and summer reach up to 20 - 23cm while those of the cohort hatched autumn and winter reached up to 25-30cm. The growth pattern of *T. pacificus* varied not only by hatching season but also by migration routes and feeding areas. In the Sea of Japan, *T. pacificus* which migrate up to subarctic waters are bigger than that migrate within Tsushima warm current region (Kidokoro and Hiyama, 1996). The variation in the growth pattern by migration areas is considered to be caused by differences in environmental conditions e.g. thermal condition, food availability (Kidokoro and Hiyama, 1996).

2.3. Reproductive Characteristics

2.3.1. Gonad Development

The maturation process in *T. pacificus* has been studied by histological observations (Takahashi and Yahata, 1973; Ikeda *et al.*, 1991a,b). Ikeda *et al.* (1991a) divided female maturation into six stages based on histological observation of ovaries. The stage composition in oocytes in ovaries of maturing females shows asynchron development. The female maturation process consists of two phases, and ovary and oviduct development are correlated with nidamental gland development. In the first phase, ripe ova are produced in the ovary with rapid development of the nidamental gland, and in the next phase, ripe ova are transferred into the oviduct and stored there until spawning. Male maturation was in five stages (Ikeda *et al.*, 1991b). Spermatozoa are produced in the testis even when the testis is relatively small, and the male maturation process consists of two phases. In the first phase, spermatozoa are produced in the testis, and in the next phase, spermatozoa are transferred into the accessory gland, where they are packed in spermatophores and stored until mating.



(From Kidokoro *et al.*, 1999).

Figure 4. The growth pattern of *Todarodes pacificus* examined based on statolith microstructure.

A clear definition of the different maturity stages is of great importance for fisheries biologists, particularly for recognizing spawning populations. Ikeda *et al.* (1991a) also showed that female maturity of *T. pacificus* is well correlated with both the gonad somatic index (*GSI*: ovary and oviduct weight as a percentage of body weight) and nidamental gland index (*m*: a ratio of nidamental-gland length to mantle length). In immature female (i.e., those in maturity stages I-III), the *GSI* is <1.0% and *m* is <0.21. In maturing female, the *GSI* is between 1.0 and 2.6% and *m* is between 0.21 and 0.29. In mature female, the *GSI* is >2.6% and *m* is >0.29. In male *T. pacificus*, Ikeda *et al.* (1991b) showed that maturity could be expressed numerically using the testis somatic index (*TSI*: testis weight as a percentage of body weight) and accessory gland somatic index (*AGSI*: accessory gland weight as a percentage of body weight). These numerical values are *TSI*>0.5% and *AGSI*>0.1% in the maturing stage, when there are no spermatophores and the vas deferens is white, and *TSI*>2.0% and *AGSI*>1.0% in the mature stage, when spermatophores are present in the spermatophore sac and penis.

2.3.2. Maturation, Mating and Spawning

Since 1988, Hokkaido University scientists have conducted captive experiments to clarify the reproductive characteristics of *T. pacificus* in a filtered, recirculating raceway tank (15,000 L in capacity) at the Marine Biological Station of Hokkaido University (Sakurai *et al.*, 1993). Immature squid have been collected from inshore waters of southern Hokkaido, Japan, and maintained in the tank, where they mature, mate and spawn (Sakurai *et al.*, 2003).

In cephalopods, high temperature promotes the development of the gonad of *Octopus* species and *Sepiidae* (Mangold, 1987), but little is known the physiological effect of water temperature on development of the gonads of *T. pacificus*. Song *et al.* (accepted) found the

effect of the water temperature on the maturity mechanism of *T. Pacificus* differed between the sexes in captivity.

The squid were maintained at five constant temperatures, considered to be representative of their feeding and spawning areas: 12, 13, 15, 17 and 19 °C (Song *et al.*, accepted). The results show that the effect of the water temperature on the maturity mechanism differed between the sexes (Figure 5).

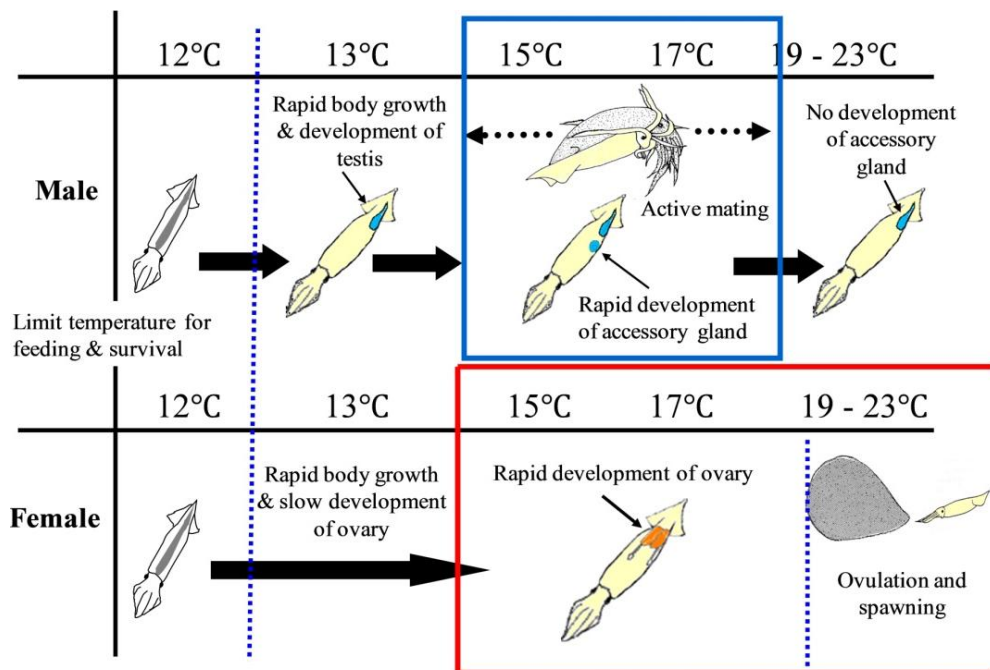


Figure 5. Effect of the water temperature on the maturity mechanism of *T. Pacificus* differed between the sexes in captivity. The squid were maintained at five constant temperatures, considered to be representative of their feeding and spawning areas: 12 , 13 , 15 , 17 and 19 °C.

Males started maturing at 13 °C and copulated frequently at 15-17 °C, but less frequently at 19 °C. Females started maturing at 15 °C, and the sexual maturation increased as water temperature rose. In conclusion, the optimum water temperature for males was 15-17 °C, but higher temperatures are suitable for the maturation mechanism of females.

During mating, the male quickly approaches the female from below and grasps her around the head and mantle. The hectocotylus (the male's fourth right arm) then picks up spermatophores and drives them into the buccal membrane of the female within a few seconds (Sakurai *et al.*, 2003). Generally a few days before spawning, females stop feeding and often rest on the tank bottom (Bower and Sakurai, 1996). While resting, their chromatophores flash rapidly over the entire body surface; this characteristic is now known to be a sign that spawning is imminent. Spawning has been observed only once (Sakurai *et al.*, 2003). The female's arms just prior to spawning were slightly flattened and lowered. After one minute in this posture, the arms opened gradually, allowing the small egg mass to be formed and held within the arms. The egg mass expanded and was not clearly visible during the spawning. Egg-mass formation resembled the swelling of a balloon and lasted about seven minutes. The spawning behavior and property of egg mass were similar to those of *Illex*

illecebrosus ((Durward *et al.*, 1980, O'Dor *et al.*, 1982, O'Dor and Balch 1985, see Chapter 13). The results of our captive experiments suggest that mature females usually spawn once and then die, but some females spawned twice in a week when their spawning was disturbed (Ikeda *et al.*, 1993).

2.3.3. Egg Mass and Fecundity

No naturally spawned egg masses of *T. pacificus* had ever been found in the spawning ground, but a laboratory study revealed the complete property of the egg masses (Bower and Sakurai, 1996). The egg masses spawned from reared females were gelatinous, spherical, nearly neutrally buoyant. Externally, the masses were covered with a jelly-like secretion, presumably from the nidamental glands, and the interior of the masses consisted of a jelly presumably secreted by the oviducal glands. Eggs were positioned 0.4-2.0 cm apart throughout the inner mass and the chorion surrounding each egg expanded to diameters of 1.9-2.3 mm. The egg-mass surface layer effectively prevented crustaceans, protozoans, and bacteria from infesting the masses. An egg mass with diameter 80 cm contained *ca.* 200,000 eggs and more than 90% of the eggs were fertilized. Paralarvae hatched 4-6days (18-23°C) and the egg masses disintegrated soon after hatching. Paralarvae swim vertically out of the egg masses and no paralarvae remain within the masses.

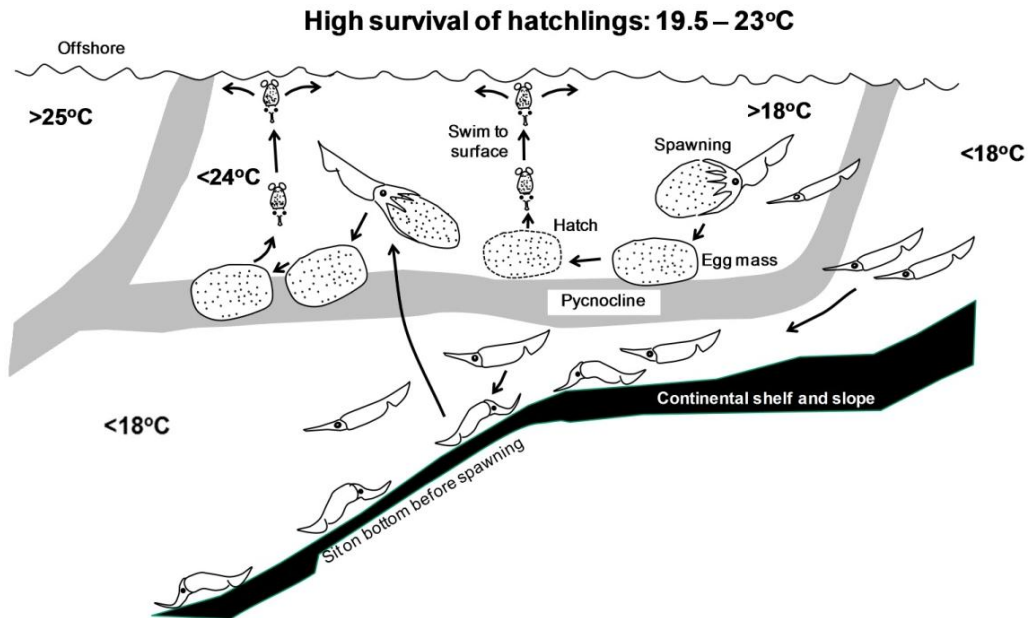
The fecundity of *T. pacificus* based on counts of ripe ova in oviducts of pre-spawning females is estimated to be between 320,000 and 470,000 (Soeda, 1956). However, in the ovaries of spawning females, oocytes occurred in all stages of development, from yolkless to mature stages and in exhausted females with thin mantles, the ovary and oviducts composed 28 % of the total body weight (Ikeda *et al.*, 1993a). The oviducts of dead post-spawning females still contained many ova (Bower and Sakurai, 1996) suggesting that females do not necessarily spawn all ova before dying.

2.3.4. Hypothesis of Reproduction Process

Based on the laboratory studies, a hypothetical process in the early stage was proposed by Sakurai (2006; Figure 6) which revised the similar hypothesis by Sakurai *et al.* (2000).

Spawning is assumed to occur above the continental shelf and slope around Japan, because captive females regularly sit on the tank bottom just before spawning (Bower and Sakurai, 1996). Also bottom trawls often collect exhausted spent females on the continental shelf and slope at 100-500 m depth (Hamabe and Shimizu, 1966).

By combining results from field surveys and captive experiments, Sakurai *et al.* (2000) proposed the following reproduction process. After sitting on the bottom the adult squid swim to an upper layer and spawns in surface water above thermocline. The spawned egg masses, due to differences in density, sink until reaching a buoyancy depth above thermocline. Once hatched the hatchlings will swim to the surface and are transported to the respective feeding grounds by the currents. Laboratory experiments have shown that higher hatchling survival rates and swimming activities are obtained when the water temperature range between 19.5°C and 23°C (Yamamoto *et al.*, 2012), while most hatchlings collected off southern Japan occur at sea surface temperatures of 17-23 °C (Bower *et al.*, 1999).



(Modified from Sakurai *et al.*, 2000, Sakurai, 2006).

Figure 6. New schematic view of reproductive processes of Japanese common squid, *T. pacificus*.

3. Ecology

3.1. Distribution and Abundance

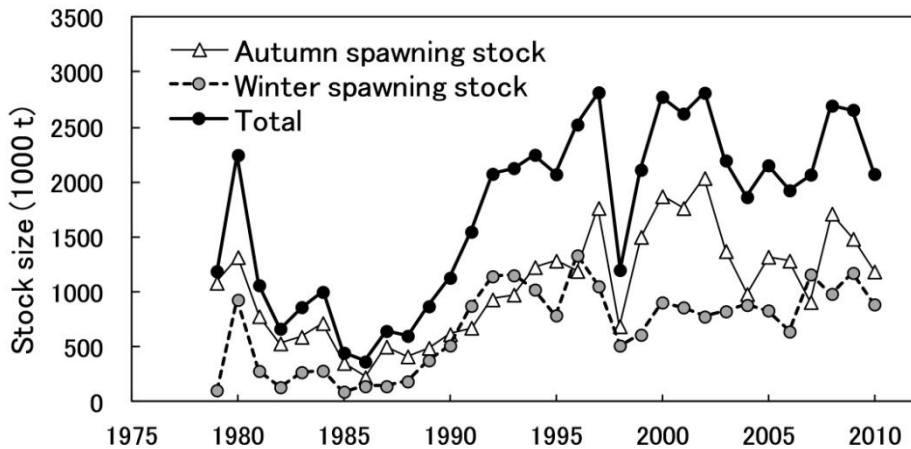
T. pacificus is distributed mainly in the northwest Pacific along the Japanese Island including the East China Sea, the Sea of Japan and the southern Okhotsk Sea (Figure 1). The distribution range shifts seasonally with changes in temperature. The distribution range usually expanded up to 50N° in September, but it is about 40N° in April. The abundance of the *T. pacificus* is assumed to be varied on a decadal scale. It was estimated at about 2 – 3 million tons around Japanese Island during 1990s and 2000s, but it was estimated below 1 million ton in the 1980s (Figure 7).

3.2. Temporal Variations

The distribution range, migration patterns and spawning grounds of *T. pacificus* were varied with changing stock size based on the observations over 50 years, which are assumed to be caused by changing oceanographic conditions.

The distribution range on the Pacific side of Japanese waters shrunk with the decline of the stock size of winter spawning stock during the 1970s and 1980s, and fishing ground east of Hokkaido Island disappeared (Nakata, 1993). Basically, the winter spawning stock migrates around the Japanese Islands counterclockwise, but such migration pattern was not observed in this period (Nakata, 1993). The distribution range had expanded to the same range which was observed during the 1950s and 1960s on the Pacific side of Japanese waters,

with the rebound of the stock size of winter spawning since 1990s. It was indicated that the main spawning grounds of the autumn spawning stock expanded coincided with 1989 regime shift based on the paralarval survey in the Sea of Japan (Goto, 2002; Kidokoro *et al.*, 2010). In the Sea of Japan, not only spawning grounds but also spawning migration patterns have changed coincided with 1989 regime shift (Kidokoro *et al.*, 2010). The migration patterns of the autumn-spawning stock can be summarized into two patterns based on oceanographic conditions or stock size. During warm oceanographic conditions (in the 1960s and 1990s), the autumn-spawning stock moved towards the Korean Peninsula and the Tsushima Strait, but during cold oceanographic conditions (in the 1980s), the autumn-spawning stock moved towards the central part of Honshu Island (Kidokoro *et al.*, 2010).



(From Kidokoro *et al.*, 2011; Yamashita and Fukuwaka, 2011).

Figure 7. Estimated stock size of *Todarodes pacificus*.

3.3. Feeding Ecology

T. pacificus is a generalist rather than specialist predator, feeding opportunistically and take whatever is available. The squid feed on zooplankton and small fish, including juvenile walleye pollock *Theragra chalcogramma* with the consumption of pollock by squid on the Oyashio Shelf during autumn being sufficient to affect pollock recruitment (Sakurai, 2007). Prey items of *T. pacificus* vary by region, but crustaceans, fish and squids are generally dominating the diet (Hamabe and Shimizu, 1966; Okiyama, 1965; Okutani, 1962). Crustaceans are mainly composed of copepods, amphipods and euphausiids. Okutani (1962) has been reported that brachyuran decapod larvae (megalopa) were predominant prey in the Pacific coast of central Japan. It has also been reported that *T. pacificus* ingested other zooplankton taxa such as ostracods and chaetognaths, but they were of limited importance (Okutani, 1962; Uchikawa and Kidokoro, 2011). Various fish such as Japanese ancovy *Engraulis japonicus*, Pacific saury *Cololabis saria*, myctophids, *Mauloricus japonicus* and juvenile walleye pollock are recorded from the stomach contents (Hamabe and Shimizu, 1966; Hashimoto and Ishito, 1991 Okiyama, 1965; Okutani, 1962). The broad breadth of the feeding spectrum of fish prey may reflect regional prey availability. *T. pacificus* feeds other

squids such as firefly squids *Watasenia scintillans* and its own species (cannibalism) (Araya, 1967; Hamabe and Shimizu, 1966; Kidokoro and Uji, 1999; Okiyama, 1965). In cannibalism of *T. pacificus*, it has been reported that larger (>120 mm ML) individuals fed on smaller (<50mm ML) ones (Kidokoro and Uji, 1999). Cannibalism in *T. pacificus* appears to occur frequently when squid of a wide size range distribute sympatrically. *T. pacificus* also feed on benthic organisms (Hamabe and Shimizu, 1966; Tanaka, 1993). In the Sea of Okhotsk, *T. pacificus* caught by bottom trawls during daytime over the continental shelf has been reported that polychaetes were the most frequent prey (Tanaka, 1993). This suggest that *T. pacificus* will be associated with the sea bottom in shallow sea topographies such as continental shelf, islands and seamounts, and benthic prey may be more important in their diet during daytime near the bottom.

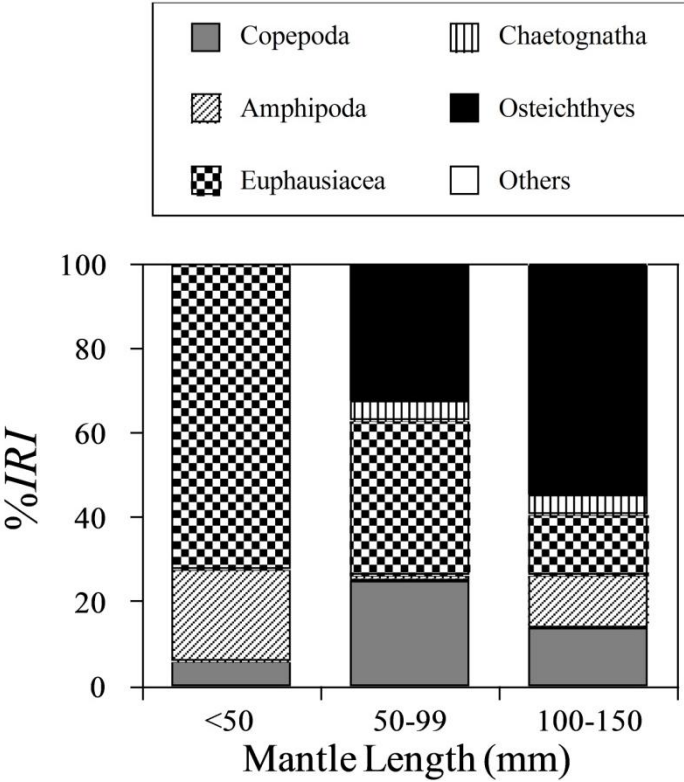


Figure 8. Diet of juvenile (<150mm ML) *Todarodes pacificus* in the Sea of Japan during spring. Based on data from Uchikawa and Kidokoro (2011), an index of relative importance (IRI) (Pinkas *et al.*, 1971) was calculated for each prey taxon as $IRI_i = F_i \times (N_i + W_i)$, where *i* represents *i*th prey taxon, *F* is the percentage frequency of occurrence, *N* is the percentage number and *W* is the percentage wet mass. The IRI for each major group of prey taxa was then standardized to %IRI (Cortés, 1997) as $\%IRI_i = 100 \times IRI_i / \sum IRI_i$.

Changes in diet during ontogeny have been described in *T. pacificus*. Uchikawa and Kidokoro (2011) have reported that details of prey composition of juvenile (<150mm ML) *T. pacificus* based on gut content analysis in the Sea of Japan during spring (Figure 8): squids smaller than 50mm ML feed exclusively on crustaceans such as copepods, amphipods and euphausiids, and then shift to crustaceans and fish at ML of 50-99mm; after reaching a ML of

100mm, fish was the most important prey and crustaceans were less important. Squids larger than 150mm ML mainly feed on fish and squids (Hamabe and Shimizu, 1966), although amphipods (*Themisto japonica*) and euphausiids (*Euphausia pacifica* and *Thysanoessa longipes*) dominated in the diet of squids larger than 150mm ML in offshore waters of the Sea of Japan (Uchikawa, personal observation).

The first prey of *T. pacificus* paralarvae is not known. It has been postulated that paralarvae of ommastrephids might suspension feeder (O'Dor *et al.*, 1985) and prey capture begins after the proboscis divides (Shigeno *et al.*, 2001; Uchikawa *et al.*, 2009). It was also suggested that beak protrusion might signal the beginning of raptorial feeding in ommastrephids (Uchikawa *et al.*, 2009). Like neon flying squid *Ommastrephes bartramii* (Uchikawa *et al.*, 2009), the first prey of *T. pacificus* paralarvae is presumably small zooplankton such as copepods. However, no information is available on its feeding habits. To understand the early life stages of *T. pacificus*, information about early feeding ecology such as first prey, feeding behavior and development of feeding apparatus are still wanting.

3.4. Predators

T. pacificus was preyed upon in great numbers by large fish such as mackerels, *Scomber japonicus*, *S. australasicus*, yellowtail, *Seriola quinqueradiata*, bluefin tuna, *Thunnus thynnus*, sharks, and by marine mammals such as dolphins through its life cycle. In the Sea of Japan, about 40 individuals freshly consumed *T. pacificus* were found in stomachs of Dall's porpoise collected throughout the day in summer and autumn (Ohizumi *et al.*, 2000). The minke whale, *Balaenoptera acutorostrata* is widely distributed throughout the world. In the western North Pacific, the minke whale is an opportunistic feeder with a broad diet and flexible feeding habits.

The daily consumption of a mature minke whale is 200 kg (Tamura and Fujise, 2002). On the Pacific side of Japan, this species feeds mainly on Japanese sardine, *Sardinops melanostictus*, Japanese anchovy, *Engraulis japonicus*, Pacific saury, *Cololabis saira* and *T. pacificus* (Tamura and Fujise, 2002).

3.5. Parasites

Larval anisakid nematodes are the most famous parasites of *T. pacificus*. They are infected by two species of third-stage larvae of anisakid nematodes. The larvae of *Anisakis simplex* s.l. (henceforth referred to as *A. simplex*) were commonly found in the outside walls of stomach and caecum of *T. pacificus*, whereas the larvae of *Lappetascaris* sp. were found in the anterior end of mantle (Nagasawa and Moravec, 1995; Takahara and Sakurai, 2010).

A. simplex is one of the common nematodes in marine fishes and squids. The life cycle involves several hosts (Figure 9, Sakanari and McKerrow, 1989; Nagasawa, 1990, 1993; Audicana and Kennedy 2008). One paratenic host is *T. pacificus*, a commercially important species comprising two main cohorts (autumn and winter) that have different migration routes and feeding areas.

The prevalence of *A. simplex* is higher in the winter cohort than in the autumn one (Takahara and Sakurai, 2010), presumably because the winter cohort forages in the Sea of

Okhotsk and the Oyashio regions (northwest Pacific Ocean), while the autumn cohort does not migrate to these areas (Sakurai *et al.*, 2000). This suggests that infection occurred when *T. pacificus* fed on infected prey (e.g., euphausiids, walleye pollock) in the Sea of Okhotsk and the Oyashio region.

According to Uchida *et al.* (2006), *A. simplex* in the coast of Japan was classified in *A. simplex sensu stricto* and *A. pegreffii*. In addition, 100% of the larvae collected from coast of Hokkaido and 94% of adults collected from Western North Pacific Ocean were identified as *A. simplex s. str.* On the other hand, 97% of the larvae collected from coast of Kyushu Island prefecture were identified as *A. pegreffii*. As a result, *A. simplex s. str.* is primarily distributed in the North Pacific Ocean and *A. pegreffii* is primarily distributed in the southern Sea of Japan. As a result of this and Takahara and Sakurai (2010), it is thought that *T. pacificus* are infected by *A. simplex s. str.*.

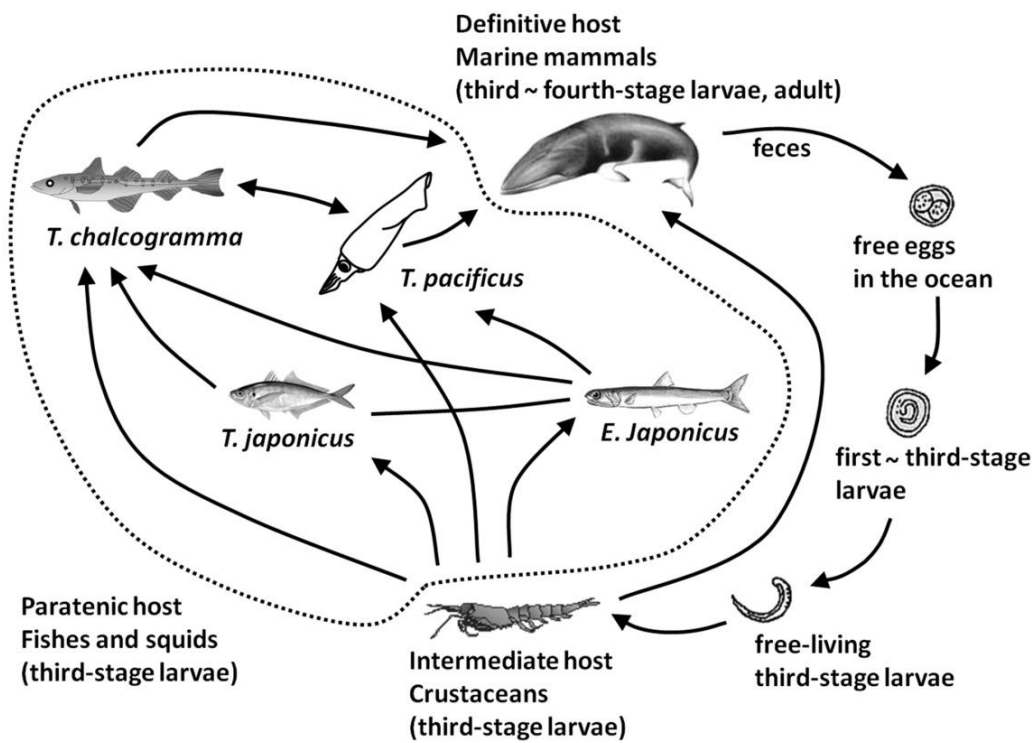


Figure 9. Life cycle of *Anisakis simplex*.

The prevalence of *Lappetascaris* sp. is high in both cohorts at the feeding grounds near Hokkaido, which suggests this is where infection occurred. But the life cycle of *Lappetascaris* sp. is not known.

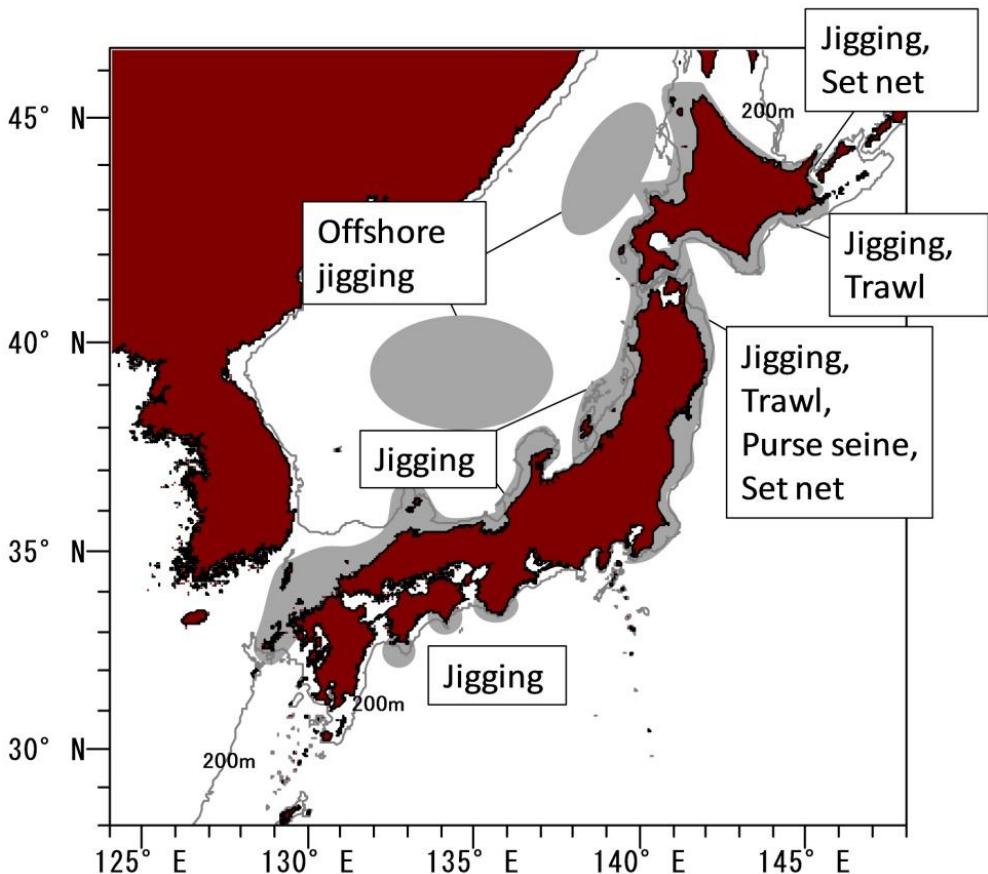
The definitive host of this species is thought to be a predator marine fish (Nagasawa and Moravec 1995), which was probably fed on by *T. pacificus*, so it is unclear how and where these larvae came from.

4. Fisheries

4.1. Stock Definition

Basically, *T. pacificus* is divided into two or three stocks by spawning season (Araya, 1967; Okutani, 1977; Osako and Murata, 1983; Kidokoro *et al.*, 2003). In general, units for stock assessment are divided into geographical regions, and catch statistics for each stock are totaled in each region. But for *T. pacificus*, the catch statistics of each stock are divided based on the differences found in the fishing grounds throughout the seasons by using the monthly catch statistics (Kidokoro *et al.*, 2003), which also include landings from South Korean fisheries.

It must be noted that the methods (including the definition of the stock units) are being currently used for stock assessment in Japan, but there are no agreements or discussions with South Korean researchers or their government.



(Modified from Yamashita and Mori 2009).

Figure 10. Major fishing grounds and fishing methods for *Todarodes pacificus* around the Japanese waters.

4.2. Fishing Methods and Fishing Grounds

4.2.1. Japanese Fisheries

T. pacificus is fished by using several fishing methods. *T. pacificus* is mostly fished by jiggers. However, the characteristics of fishing methods have variations among the regions in Japan (Figure 10). *T. pacificus* is mostly fished by coastal jiggers and offshore jiggers in the Sea of Japan. The catches in coastal areas are landed as fresh catch, and offshore catches are frozen on board then landed (Kidokoro *et al.*, 2011). Along the Pacific side of Japanese waters, *T. pacificus* is mainly taken by coastal jiggers, but more than a half of the total catch along the Pacific side is taken by other fisheries, *i.e.* offshore trawlers, large-and medium scale purse seiners and set nets (Yamashita and Fukuwaka, 2011). In the Sea of Okhotsk and the Nemuro Strait, most of the catches are taken by set nets and coastal jiggers (Sakaguchi and Sawamura, 2009). Annual catches have been changing drastically in these regions.

4.2.2. Korean Fisheries

In the Korean waters, *T. pacificus* is fished in the Sea of Japan, the Yellow Sea and the East China Sea by several fishing methods. Most of the catch is made by offshore jigging, large trawl and eastern sea trawl in those areas, recently. In the case of Japanese fisheries, the ratio of offshore and coastal jigger catches have decreased, and the ratio of trawlers catches have increased since 1990.

The fishing grounds of coastal jiggers, whose vessels are classed less than 8 tons, are along the coast of Korea (Choi *et al.*, 2002). In the fishing grounds of offshore, jiggers vessels classed the range from 8 tons to 90 tons, are mostly in the central part of the Sea of Japan and around Yamato Bank (Choi *et al.*, 2002).

4.3. Landings and CPUE

4.3.1. Landings

Total annual landing of *T. pacificus* by the Japanese and South Korean fisheries was about 500,000 t during the 1950s and 1960s, but it decreased significantly during the 1970s and dropped to 200,000 t in the mid 1980s. In the 1990s the landings increased and have rebounded to about 500,000 t in recent years. Annual catch in the Sea of Japan was approximately 100,000 – 150,000 tons during the 1950s and 1960s. It rose to 300,000 tons in the beginning of 1970s however it declined to 200,000 tons during the middle of 1970s and the 1980s (Kasahara, 1978; Osako and Murata, 1983). Annual catch in the Sea of Japan increased again in the 1990s, and has remained at approximately 300,000-400,000 tons. Annual catch in the Pacific region was approximately 300,000 – 500,000 tons during the 1950s and 1960s. It declined drastically around the beginning of 1970s, and was approximately 10,000-30,000 tons during the 1970s and 1980s. Annual catch in the Pacific region increased again in the 1990s, and has remained at approximately 100,000-200,000 tons.

4.3.2. CPUE

In the Sea of Japan, CPUE (ton/vessel/day) of offshore jiggers was mainly under 1.0 ton / vessel / day in 1980s. The CPUE increased since 1989, and were at high levels during 2000 – 2003. The CPUE are around 2.5 tons/vessel/day, recently. The operations of offshore jiggers are limited to offshore regions, thus the CPUE implies the abundance index in the offshore regions. Along the Pacific side of Japanese waters, the level of CPUE of coastal jiggers was in the range of 500 – 1,000 individuals / vessel / day, until the latter half of 1980s. The CPUE of coastal jiggers increased to a high level over approximately 2,000 ind. / vessel / day since 1990s in this region, and are around 3,000 ind. / vessel / day in recent years. The detailed catch statistics of *T. pacificus* by Japanese fisheries were described in the stock assessment reports around the Japanese waters (Kidokoro *et al.*, 2011; Yamashita and Fukuwaka 2011).

4.4. Recruitment and Environmental Variability

Low-pass filtered SST data off southwestern Japan show alternate warm and cold periods at decadal scales that correspond with the variability in the Pacific Decadal Oscillation (PDO). For example, there was a sudden decrease in SSTs in the late 1970s (shift to positive PDO) and an increase in SSTs (negative PDO) during the mid to late 1980s (Senjyu and Watanabe 2004). Note that the positive phase of the PDO corresponds to cool conditions on the western side of the Pacific and warm on the eastern side and vice versa in its negative phase. *T. pacificus* decreased during the cool regime period from the late-1970s to late-1980s (Figure 2; Sakurai *et al.* 2000, Rosa *et al.*, 2011), while Japanese sardine, *Sardinopsis japonicus* increased exponentially. Squid catch has increased after the late-1980s warm regime period (Sakurai *et al.*, 2000). These catch fluctuations are similar with those of Jack mackerel, *Trachurus japonicus* and the Japanese anchovy. After 1989, the feeding area of the winter spawning stock expanded to the Oyashio region during summer-autumn. During the warm regime period after 1989, the inferred spawning areas of the winter spawning group have occurred along the continental edge off the Kyushu Island and the Nansei Islands, and the inner flow of the Kuroshio has transported the hatchlings in the surface layer northeastward along the continental edge from the spawning areas to the nursery areas (Figure 1). However, during the cool regime of the 1980s, when winter wind stress was stronger, air temperature at the sea surface was lower, and mixed layer depth at the spawning grounds was deeper than after 1989, so the spawning areas were not connected along the continental edge.

The catch is considered a good proxy for abundance and hence reproductive success (Choi *et al.* 2008). One reason for the increased larval survival during warm periods might be related to an increase in the size of the spawning areas. In the warm periods, the autumn and winter spawning area extends northward into Tsushima Strait and farther eastward to the continental slope. For the latter, the inner flow of the Kuroshio helps transport the hatchlings into the Oyashio region to feed. Thus during warm periods more squid may be transported to the feeding grounds via this circulation. During cool periods there is less spawning along the continental slope and the squid are deeper due to an increased mixed layer depth caused by stronger winds. This may result in less squid being transported into the Oyashio region. Fluctuations in the strength of the northward flowing Tsushima Warm Current influences the area of the warm water region in the Sea of Japan, which also matches the variability in squid catches from this region (Choi *et al.* 2008). The current's effect on squid is believed to be

through its prey as the changes of annual zooplankton biomass are also closely connected to the fluctuations in the Tsushima Warm Current. This too may contribute to the increased survival of *T. pacificus* in the Sea of Japan during warm years.

4.5. Management and Stock Assessment

4.5.1. Management in Japanese Fisheries

The Japanese Fisheries Agency has adopted TAC as a method of stock management for the seven major fisheries since 1997. *T. pacificus* was added to the TAC management plan in 1998. The annual TAC is set by the government through a process that weighs a combination of socioeconomic factors and the allowable biological catch (ABC), recommended by researchers of the national fisheries research institute.

The calculations of the Japanese ABCs are modeled after those used in the U.S. (Restrepo *et al.*, 1998). ABC (ABC_{limit}) is calculated from the fishing mortality (F_{limit}) and forecasted stock abundance in the target year. The F_{limit} usually uses biological reference points (e.g. F_{msy} , F_{med} , $F_{0.1}$; see Caddy and Mahon, 1995) or current fishing mortality in the case where the current stock size is above a threshold stock size (B_{limit}). If the current stock size is below the B_{limit} , then the F_{limit} should be set below the biological reference point accordingly for rebuilding stock status to an acceptable level within an appropriate time frame (Restrepo *et al.*, 1998). The biological reference point used as the F_{limit} is revised slightly every year using data from the latest surveys.

It has become clear that not only fishing effort but also changing environmental conditions affect the size of *T. pacificus* stocks. For ommastrephid squids, annual variability in oceanographic conditions causes annual variation in recruitment strength (Dawe *et al.*, 2000; Waluda *et al.*, 2001). Moreover, decadal or inter-decadal variations or regime shifts also influence the stock status (Sakurai *et al.*, 2000). Because both human and environmental pressures cause stock size fluctuations, effective management of ommastrephid squid stocks must balance an understanding of fishing effort and environmental conditions.

4.5.2. Current Stock Assessment Methods Being Used in Japan

Change in the annual stock size of *T. pacificus* has been monitored by surveys conducted by scientific research vessels with squid-jigging machines at the beginning of the fishing season since the 1970s (Kidokoro *et al.*, 2011; Yamashita and Fukuwaka 2011). The density of *T. pacificus* at each station is estimated based on the CPUE (the number of individuals caught/squid-jigging machine/hour (ind./h)) of the research vessels, and the average CPUE of all the stations is used to calculate the annual stock index. Stock abundance is quantified based on the stock index, which is supposed to be in proportion to the stock abundance. Biological reference points are estimated based on the estimated spawner–recruit relationship which is shown in the relationship between number of recruits and spawning stock.

The change in the stock size of *T. pacificus* coincided with changing environmental conditions, and the spawner–recruit relationship is assumed to change with changing environmental conditions. In particular, decadal or inter-decadal changes are assumed to influence stock status and spawner–recruit relationship of *T. pacificus*, therefore we used the data collected since 1990 to estimate the spawner–recruit relationship (Kidokoro *et al.*, 2011;

Yamashita and Fukuwaka 2011). The parameters used in our spawner-recruit relationship are estimated from data collected since 1990 following this apparent regime shift, but when the current regime changes, these parameters should be revised accordingly. However, it is difficult to predict when regime shifts might occur.

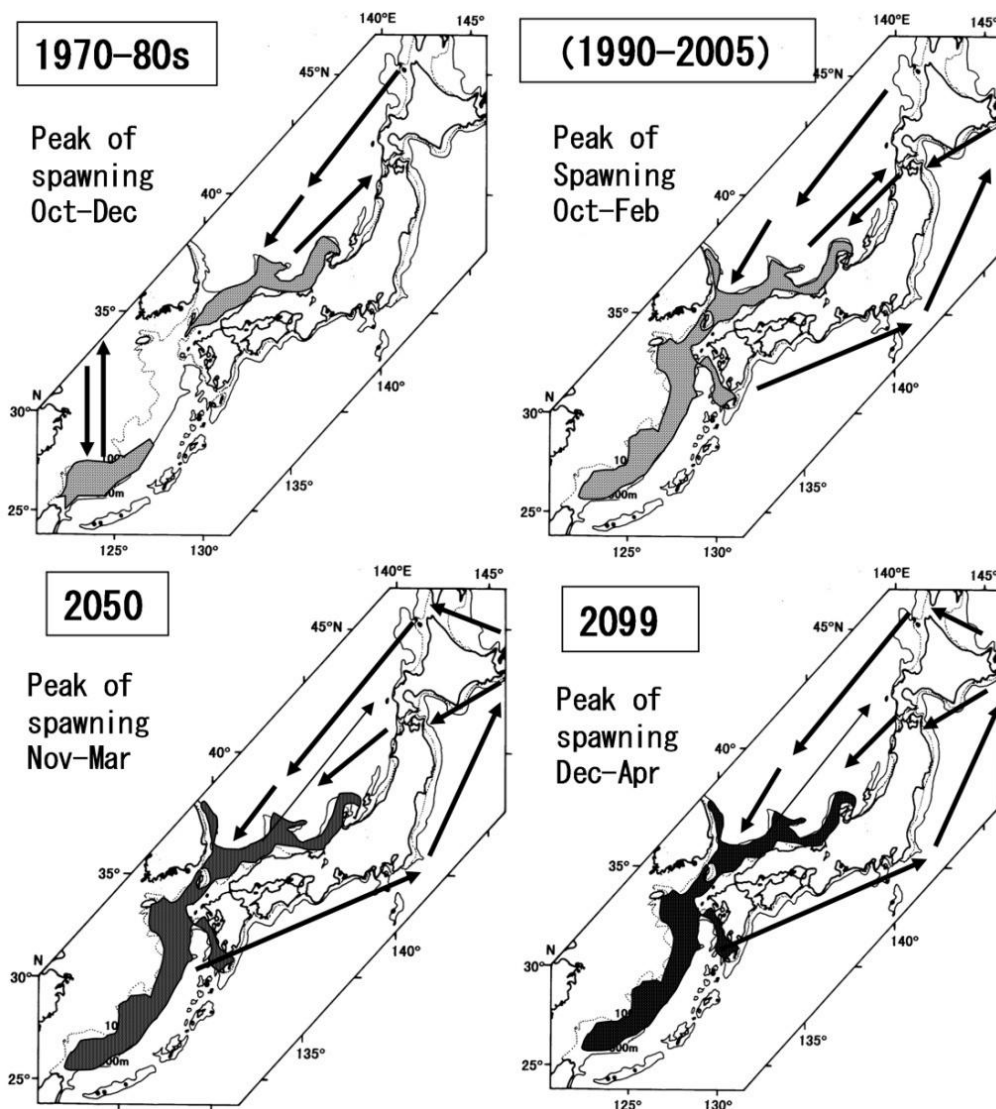


Figure 11. Predicted spawning periods, areas, and migration routes of *T. pacificus* during 1970-80s (cool regime), 1990-2005 (warm regime), 2050 (SST: 2° increase), and 2099 (SST: 4° increase). Estimated environmental changes in waters around Japan based on the IPCC global warming scenario.

4.6. How to Predict Life History Based on the Global Warming Scenario

Short and long-term change of *T. pacificus* stock can be explained and predicted by physical parameters such as wind stress, air temperature, SST, and mixed layer depth during

the spawning period based on the reproductive hypothesis. Although we cannot forecast climate change even in the next month or season, we can map the inferred spawning grounds using the SST areas between 18-24°C, especially between 19.5-23°C and within a specific range of bottom topography (100-500m depth) (Rosa *et al.*, 2011).

Based on this method, we can monitor the trend of stock fluctuation and structural change such as the recent seasonal changes of inferred spawning areas and predict the stock condition of the next year's cohort. Further, we can try to predict whether the squid will be extinct or will occupy a marine ecosystem during the 21st Century based on the Global Warming Scenario (IPCC, International Panel of Climate Change) using the Earth Simulation System (FRCGC, Frontier Research Center of Global Change, Japan).

If we examine the monthly changes of squid distribution (temperature range of distribution: 12-23°C at 50m depth) and inferred spawning areas in 2005, 2050, and 2099, the northern limit of the squid distribution shifts to the north by 1°N/50 yrs and covers the water around Hokkaido Island by 2099. The inferred main spawning grounds also move from the southern Sea of Japan and the East China Sea around Tsushima Strait to the East China Sea by 2099. The peak of the inferred spawning period will shift from October-February in 1990-2005 to November-March in 2050, and December-April in 2099 (Figure 11).

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